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OSTEOLOGY OF PHENACOCÆLUS TYPUS PETERSON.

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INTRODUCTION.

In 1906-7 the writer briefly described the Oreodont *Phenacocælus* from the material in the Carnegie Museum.<sup>1</sup> Twelve or fourteen individuals of this genus were found in the upper Monroe Creek Beds, near the head of Squaw Creek, Sioux County, Nebraska. The type (No. 1263) consists of the greater portion of a skeleton, found in an articulated position, while the rest of the material is regarded as paratypical, except one specimen, No. 1288. The latter specimen described on page 161, is provisionally regarded as pertaining to a separate species, pending the discovery of cranial and appendicular portions found together.

In the original description it was stated that certain cranial structures of *Phenacocælus* reveal affinities to *Leptauchenia* and *Cyclopidius*. From the material in the Carnegie Museum a comparative study of the cranial structure of *Leptauchenia* and *Phenacocælus* was possible, but the vertebral column and the appendicular skeleton of *Leptauchenia* were lacking. The Museum was fortunate in securing, as a loan, the very complete material of *Leptauchenia* from the authorities of the Princeton University Museum.<sup>2</sup> This material from Princeton has now enabled me to make a more complete comparison between the three genera, viz.: *Phenacocælus*, *Leptauchenia*, and *Merycoidodon*. The main object of the present

<sup>1</sup>Annals Carnegie Museum, Vol. IV, 1907, p. 29-32, Figs. 4, 5.

<sup>2</sup>Since the manuscript of this paper was first prepared, this specimen in the Princeton University Museum has been set up in an articulated position.

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paper, therefore, is (1) to present the osteology of *Phenacocælus* as completely as possible; (2) to compare the latter genus with the much older form *Merycoidodon* from the Oligocene, heretofore supposed to be more or less in the line of ancestry; and (3) to make an especial effort to ascertain the relationship between *Phenacocælus* and *Leptauchenia*. The question of the systematic position of *Phenacocælus* will follow the general osteological description and discussion of comparisons.

The illustrations are reproduced from drawings made by Mr. S. Prentice.

#### Principal Characters of *Phenacocælus typus* Peterson.

*Skull with a general Merycoidodont structure, but proportionally broader and shorter. Orbits directed more upward than in Merycoidodon culbertsoni and more nearly like those in Leptauchenia. Two elongated and narrow foramina on top of the skull, situated at the anterior part of the frontals and near the median line similar to, though smaller than, those of Leptauchenia. Presence of facial vacuities and deep lachrymal pits. Unusually deep pits on posterior face of occipital plate. Short facial region and an elongated cranium. Dentition:  $I_3^3 C_1^1 P_4^4 M_3^3$ ; hypsodont to approximately the same degree as in Leptauchenia; tympanic bulla very large and extending much below the post-glenoid process; sagittal crest low; infraorbital foramen above  $P^3$ ; nasal greatly overhanging anteriorly; limbs and feet short and heavy; metatarsals shorter than the metacarpals. Animal about the size of a domestic sheep.*

#### THE HEAD.

*The Cranium.* (Pl. XVI, fig. 31; Pl. XVII, figs. 11, 12; Pl. XIX.)—The greater part of the right maxillary, and premaxillary bones are preserved in the type, No. 1263. The skull has received considerable lateral crushing, causing an asymmetrical appearance. The occiput is of medium height, with the lambdoidal crests prominent, and a large and deep excavation on either side of the occipital plate just below the junction of the post-temporal ridge with the lambdoidal crest, similar to that found in other genera of this group (*Merychys*, *Mesoreodon*, *Pro-merycochærus*). These excavations occupy a larger portion of the occiput and cause deep lateral emarginations of the supra-occipitals, while in *Leptauchenia* the pits are not present, and the occipital plate is relatively much broader. The median supra-occipital fossa is not deep, and has rough ridges for muscular attachments, which radiate upward and outward from near the median vertical line above the foramen magnum. The condyles are set close to the base, separated inferiorly by a light narrow groove, and with rudimentary accessory facets on the basioccipitals for articulation with the atlas. The foramen magnum is well proportioned in size,

and subovate in outline. The paroccipital process is prominent, as in *Leptauchenia*, trihedral in section, separated from the condyle by a deep fissure, and closely appressed to the posterior border of the tympanic bulla, as in other Oreodonts. The basioccipital is small in transverse diameter, strongly keeled, extending anteriorly between the internal walls of the tympanic bullæ, and joining the basisphenoid uninterruptedly, thus forming an arch gently curved forward to the median pterygoid fossa. The condylar foramen is of large size and is located close to the anterior base of the condyle. The parietal is an elongated, narrow, and wing-shaped bone, the extreme anterior border of which reaches very nearly to the base of the postorbital process of the frontal; the fronto-parietal suture then continues obliquely upward just back of the temporal ridge and unites with its fellow, as in *Merycoidodon culbertsoni*,<sup>3</sup> and most Oreodonts. The sagittal crest, however, is not so prominent as in the Oligocene genus, and the brain-case, as a whole, is fully as large, while the skull represents a smaller animal. The posterior wing of the parietal is not so greatly produced as in *M. culbertsoni*. In this respect it is intermediate between the latter species and *Merychyus arenarum*. Along the parieto-squamosal suture there is a very prominent ridge, which separates the temporal fossa into a shallow superior and a deeper inferior portion; there is a large foramen situated in this suture posterior to the middle of its course.

The temporal region is quite like that of *Merychyus*. Superiorly, the squamosal extends higher up upon the side of the cranium than in the latter genus, but the shape and position of the zygomatic process, the large external auditory meatus and tympanic bulla, and the closely appressed paroccipital process of the posterior border of the bulla are characters showing great similarity. In *Leptauchenia* and *Cyclopidius* the zygomatic process is more expanded laterally, and does not extend so far forward; the external auditory meatus is relatively larger and is on an even transverse line with the lambdoidal crests and the inion; while the tympanic bulla is fully as large proportionally and the paroccipital process equally appressed to its posterior border as in *P. typus*. The post-glenoid process is heavier than in *Merychyus*, but the tympanic bulla extends much below the process, though not nearly as much as in the latter genus. The glenoid cavity is large, it is convex fore-and-aft on the anterior two-thirds; further back it is concave in the same direction; the anterior face of the post-glenoid process has a comparatively less distinct transverse articular surface for the condyle of the lower jaw than is seen in *Merychyus* and *Leptauchenia*. The tympanic bulla is, as intimated above, of relatively

<sup>3</sup>A skeleton of this species in the Carnegie Museum, No. 1391, which is very nearly complete, is used for comparison in this work.

enormous size; it is relatively very nearly as great as in *Leptauchenia* and *Cyclopidius*, and in shape it is also somewhat similar to what is seen in those genera.<sup>4</sup> In some of the individuals at hand, the pit for the tympano-hyal is quite large, while that in the type is rather small, and located at the antero-external angle of the base of the paroccipital and the postero-external border of the bulla. The type is much crushed in the region of the basi- and pre-sphenoids; the foramen ovale is, however, observed to be close to the anterior extremity of the tympanic bulla. The pterygoid process of the sphenoid is well developed and extends well down, so as to form a deep median pterygoid fossa. The anterior border of the posterior narial opening is indicated as being well forward in the type. In No. 1276 of the same species the posterior narial opening is complete; its anterior margin is V-shaped, with the apex on an even transverse line with the posterior end of the alveolar border of the maxillaries. Fortunately the right frontal bone is preserved in the anterior median region, so that the external border of the frontal opening is partly preserved. This opening is an extraordinary feature of this genus and most nearly recalls that of *Leptauchenia* and *Cyclopidius*. The vacuity extends farther back than in *Leptauchenia* and is equally as far back as in the latter genus, but does not, however, extend so far anteriorly, and is very much smaller in size. Its function was no doubt the same as that in the genera mentioned. The supra-orbital foramen (in No. 1276) is closer to the posterior border of the frontal vacuity than in *Leptauchenia* and *Cyclopidius*. While the posterior boundary of the frontal is not unlike that in the Oreodonts generally, the anterior region (No. 1276) presents some very peculiar characters, *i. e.*, the narrow and elongated tongue of bone along the median line, which borders the frontal vacuity internally, joins its fellow on the median line, and comes in contact with the nasal anteriorly. The most anterior portion of the frontal is only 21 mm. from the anterior narial opening; from this point the fronto-nasal and fronto-maxillary and lachrymal sutures are only slightly diverging, so as to form a spear-shaped process like that in other Oreodonts. The external border of this process is abruptly convex, due to the large and deep infra-orbital fossa and the facial vacuity. Superiorly the frontals are rather flat, with the temporal ridges less developed than in *Leptauchenia*, and about as prominent as in *Merycoidodon culbertsoni*. The anterior border of the postorbital process has a greater backward tilt than in Oreodonts generally, and more nearly suggests that of *Leptauchenia* and *Cyclopidius*. The process is well developed, and, as in other contemporaneous genera, joins the jugal

<sup>4</sup>In one individual, No. 1278, the tympanic bulla is proportionally small, which indicates either variation, or a specific character.

process from below, completely enclosing the orbit. The superior border of the orbit is rather smooth and the orbital wall of the frontal gives to the eye an upward look as in *Leptauchenia*. The orbit is subcircular in outline.

*The Facial Region.* (Pl. XVI, fig. 31; Pl. XVII, figs. 11, 12.)—The palatine of the type is entirely wanting, but in No. 1276 this region is beautifully preserved. The maxillo-palatine suture is U-shaped, with the rounded apex in front, reaching as far forward as the molar teeth. Thus the maxillary forms a considerable part of the hard palate. The posterior nares, as above stated, are of an open V-shape; the anterior apex is even with the back part of the alveolar border of the maxillary.

Externally the maxillary of the right side of the type is complete from the back to a little in front of the infra-orbital foramen; at this point the bone is broken off, but the most anterior part of the maxilla, including the root of the canine and a fragment of the premaxillary in position, is present, though disconnected. Antero-posteriorly the alveolar border is convex, very similar to that of *Merychys elegans*. The infra-orbital foramen, however, is further forward in the present form than in *M. elegans*, and approaches the condition found in *Leptauchenia*. The external wall of the muzzle is inflated by a heavy and broadly convex ridge, which extends obliquely along the face, thus separating the side of the muzzle into two fossæ; the supra-posterior larger and deeper than the antero-inferior. The ridge for the masseter muscle is not strongly developed. In No. 1276 the palatine portion of the maxillary plate is slightly arched from the alveolar border to the median line, especially anteriorly. The posterior palatine foramen is of moderately large size; it is close to the alveolar border opposite P<sup>4</sup>. The anterior border of the palatine is emarginated for the large round anterior (palatine) foramen.

The premaxillary is relatively less robust than in *M. culbertsoni* and approaches more nearly the condition in *Merychys*. The horizontal bars separating the large anterior palatine foramina are usually broken off; when present, they are very delicate, as in *Leptauchenia*. The ascending process of the premaxillary is stronger, but does not extend so high up upon the anterior nares as in *Leptauchenia* and *Cyclopidius*; thus forming the anterior narial border from below for only two-thirds of the distance to the nasals. In *Merycoïdodon* the premaxillary touches the nasals, while in *Merychys leptorhynchus* it furnishes less of the border than in the present genus. The premaxillary is always distinctly separated from the maxillary by a suture and not completely coalesced with it, as in *Merycochærus* and *Promerycochærus*.

The jugal reaches well forward on the side of the face and is relatively heavier

below the orbit than in *M. culbertsoni*, though not so deep as in *Merychys* or *Leptauchenia*. The bone is much expanded transversely;<sup>5</sup> its anterior portion forming a prominent part of the inflated ridge of the muzzle above described. The zygomatic process of the jugal is bifurcated in the usual manner for the reception of the squamosal process; the lower part forming a suture with the inferior border of the squamosal process, and reaching back very nearly to the glenoid cavity; while the upper prong is much shorter. The postorbital process of the jugal is proportionally as well developed as in the *Agriochæridæ* generally.

The lachrymal takes up a considerable portion of the side of the face, but the area is almost entirely occupied by the large and deep lachrymal fossa above described. The superior border is emarginated for the facial vacuity. Inferiorly the jugo-lachrymal suture is quite plain and indicates that the lachrymal furnished a considerable part of the anterior border of the orbit. There is a large lachrymal tubercle, and the lachrymal foramen is below this tubercle and very close to the border, but within the orbit.

Unfortunately the nasals are entirely wanting in the type. While other specimens in our series have this region complete Nos. 1276 and 1277 are the best preserved and present interesting features. From the illustration (Pl. XVII, fig. 11) it is seen that they greatly extend in front, more or less as in *Promerycochærus carrikeri*; laterally they are imperfectly elliptical, while posteriorly they present two parallel and lance-shaped processes, thus forming a serrated suture with the median processes of the frontal (See Pl. XVII, fig. 11). The nasals are not affected from the frontal vacuities as in *Leptauchenia*, and are on the whole more like those of *Merychys*; the length, however, seems to have been subjected to a much smaller evolutionary reduction than in the Merycoidodonts generally.

*The Mandible.* (Pl. XVI, fig. 31; Pl. XIX.)—The lower jaws of the type are represented by the back part of the ascending ramus and the symphysis. The symphysis is deep and strong. The posterior border of the angle is evenly rounded below the inferior sigmoid notch. The latter is rather shallow. The condyle is very slightly injured internally, but indicates that it did not have a great transverse diameter. On the postero-internal face is a broad and plane facet, which extends well down, and the external angle overhangs the temporal fossa in the usual manner seen in other genera. The latter fossa is large and quite deep, but apparently did not extend much below the horizontal line of the teeth, as is characteristic of *Leptauchenia* and most genera of the *Agriochæridæ*. The coronoid process rises steeply; it is in size of the usual proportions, and terminates in a rounded point,

<sup>5</sup>In the type this region has received much lateral crushing.

which projects slightly backward. The superior sigmoid notch is relatively as deep as in *Merycoiododon culbertsoni*.

The lower jaws of No. 1335 are well preserved. They are as heavy as in *M. culbertsoni*, but much shorter; the horizontal ramus is deep, but in the symphyseal region the two rami are more spout-shaped. There is a large mental foramen below P<sub>3</sub>. Posteriorly below the temporal fossa the ramus is very convex from above downward; the inferior border being quite strongly flexed inwardly as in *Leptauchenia*. The symphysis is strong, as in the type specimen, and the coronoid process rises quite steeply. The temporal fossa is large and the angle rounded. The lower jaws are on the whole perhaps more like those of *Merychius* than *Leptauchenia*.

MEASUREMENTS.	Type No.	
	1263	No. 1276
Greatest length of the skull.....	185*mm.	192 mm.
Length from condyles to incisors.....	170*mm.	175 mm.
Length from posterior border of orbit to the incisors.....	102*mm.	98 mm.
Length from posterior border of orbit to the condyles.....	80 mm.	87 mm.
Length of alveolar border of maxillary.....	95*mm.	92 mm.
Length from posterior end of alveolar border to the condyle <sup>6</sup> .....	75 mm.	81 mm.
Greatest transverse diameter of the skull.....	100*mm.	112*mm.
Transverse diameter of condyle.....	28 mm.	33 mm.
Greatest transverse diameter of brain cavity.....	45 mm.	52 mm.
Transverse diameter of frontals at middle of orbit.....	42*mm.	49 mm.
Greatest transverse diameter of muzzle at anterior nares.....		35 mm.
Transverse diameter of the palate at base of incisors.....		18 mm.
Transverse diameter of palate at P <sup>1</sup> .....		23 mm.
Transverse diameter of palate at M <sup>1</sup> .....		33 mm.
Transverse diameter of palate at M <sup>3</sup> .....		33 mm.
Transverse diameter at base of post glenoid processes.....	70*mm.	81 mm.
Transverse diameter of post glenoid process at base.....	10 mm.	16 mm.
Antero-posterior diameter of post glenoid process at base.....	9 mm.	9 mm.
Antero-posterior diameter of tympanic bulla.....	28 mm.	28 mm.
Transverse diameter of tympanic bulla.....	16 mm.	19 mm.
Antero-posterior diameter of the orbit.....	28*mm.	28*mm.
Vertical diameter of the orbit.....	27*mm.	27 mm.
Vertical diameter of jugal below middle of orbit.....	16 mm.	17 mm.

MEASUREMENTS OF MANDIBLE OF NO. 1335.

Greatest length of mandible.....	137 mm.
Length of alveolar border of mandible.....	91 mm.
Vertical diameter of angle at condyle.....	72 mm.
Vertical diameter of angle including coronoid process.....	82 mm.
Vertical diameter of angle at M <sub>3</sub> .....	35 mm.
Vertical diameter of angle at P <sub>3</sub> .....	28 mm.
Transverse diameter at base of P <sub>1</sub> , both rami included.....	26 mm.

\*Indicates approximate measurement.

<sup>6</sup>The fore-and-aft crushing of the skull causes the apparent shortness of this region in the type.

*Superior Dentition.* (Pl. XVI, fig. 31; Pl. XVII, fig. 1.)—The incisors of Nos. 1277 and 1335 perhaps resemble those of *Merychys elegans* more closely than *Leptauchenia*. The basal cingula on the posterior face of the crowns are less developed than, for instance, in *M. culbertsoni*. The crowns are rather short and the teeth are set very close together in the alveolar border. The canine has the same characteristic trihedral cross-section, which obtains in the true *Merycoidodonts*; antero-internally are the two grooves separated by the sharp edge, which extends parallel with the long axis of the teeth, antero-externally it is convex fore-and-aft, while posteriorly it is vertical and straight by wear with the anterior face of P<sup>1</sup>. The tooth has a strong fang, which causes a prominent eminence opposite to the root on the lateral wall of the muzzle. The first premolar is separated from the canine by a short diastema; the tooth is placed obliquely in the alveolar border, as in *Merychys* and other genera of the family. The proportional reduction in size of this tooth is greater than in *Merycoidodon*; it is somewhat similar to what occurs in *Ticholeptus*, and not nearly so great as in *Leptauchenia* or *Merychys*. The crown is quite hypsodont and the protocone is shifted further forward on the crown, displaying in these particulars marked difference from the older genus *Merycoidodon*.

The second premolar is present in the type and is of the same relative size as in the Oligocene genus *Merycoidodon*. The characters of the tooth, however, are distinctly marked and are easily distinguished from the latter genus; that is, the external face of the tooth in the present genus has a more even surface, with a much less developed median vertical ridge, and the apex of the protocone is more anterior on the crown, more closely approaching that of *Merychys* and *Leptauchenia*. On the anterior face there is a narrow groove bounded at the bottom by a delicate cingulum; the groove is separated from a larger internal cavity by a sharp, vertical ridge, which extends nearly to the apex of the crown, while in *Merycoidodon* the ridge is confined more closely to the base. In the type the internal face of the crown is much worn, so that these characters of the tooth are less distinct, but No. 1335 shows these features more perfectly. There is a second ridge, sometimes less sharp and less developed (the deuterococone), which separates the antero-internal cavity from a much larger posterior fossa; this ridge in *Merycoidodon* is always the more prominent of the two ridges. The posterior fossa is bounded by a heavy cingulum internally and by a long, sharp crest externally. The tooth is quite obliquely set in the alveolar border. P<sup>3</sup> is much damaged in the type. Externally the crown is convex antero-posteriorly with little or no evidence of a median vertical ridge; the apex of the protocone is placed well forward on the crown, and the tooth in detail appears to be rapidly assuming the characters met with in *Merychys*. P<sup>4</sup> presents



characters altogether similar to those in the latter genus; that is to say, the crown is hypsodont, with a considerable antero-posterior concavity of the external face; the inner crescent is less strongly developed, so that in a less worn tooth it appears more like a very strong cingulum, with a widely gaping interspace between the outer and the inner crescents. The internal cingulum is only very faintly represented. Molars one and two are damaged on their internal faces. The external faces more closely resemble such genera as *Cyclopidius*, *Ticholeptus*, and *Merychius*, the median vertical ridges being directed forward to a greater degree, and the concave portions extending less obliquely inward and downward than in *Merycoidodon*. In No. 1335, which has the teeth best preserved, there is a slight anterior and posterior cingulum on M<sup>1</sup>, while externally it is faintly represented and internally entirely wanting. This is also true of M<sup>2</sup>. M<sup>3</sup> is practically complete. It is relatively much longer and narrower than in *Merycoidodon*, and in this respect holds an intermediate position between that genus and *Merychius*. Characters which closely parallel those in, for instance, *Leptauchenia* and *Merychius* are: the more antero-posteriorly compressed and forwardly extended external ribs or buttresses; the great hypsodonty of the teeth; the vertical position of the external faces of the external crescent; and the deeper and more vertically walled interspaces between the outer and inner crescents.

## MEASUREMENTS SUPERIOR DENTITION.

	Type No.
	1263
Antero-posterior diameter of the superior dentition, approximately. ....	97 mm.
Antero-posterior diameter of premolars two, three and four.....	33 mm.
Antero-posterior diameter of molar series.....	48 mm.
Antro-posterior diameter of P <sup>2</sup> .....	12 mm.
Transverse diameter of P <sup>2</sup> , approximately.....	6 mm.
Antero-posterior diameter of M <sup>3</sup> .....	20 mm.
Transverse diameter of M <sup>3</sup> .....	14 mm.

*Inferior Dentition.* (Pl. XVI, fig. 31; Pl. XVII, fig. 2.)—The inferior dentition of the type is represented by the roots of the incisors, canine, and portions of the crowns and the fangs of the first and second premolars.

The incisors are very little, if at all, reduced in size, when compared with those of *Merycoidodon*. The canine is incisiform as in the Oreodonts generally. P<sub>1</sub> was of rather small size, which may indicate a sexual character. The tooth is set obliquely in the alveolar border; the anterior edge of the crown is preserved and indicates a lance-shaped structure, which is better shown in more complete specimens. P<sub>2</sub> is even more obliquely set in the jaw than P<sub>1</sub> and has two strong roots; the antero-internal face of the crown is preserved, and shows characters similar to those of the preceding tooth.

In No. 1335 the inferior dentition, excepting the incisors and canine, is complete.  $P_1$  is more robust in this specimen than in the type. The tooth is convex externally, has a stronger vertical ridge on the inner face, sharp anterior and posterior edges, and the apex ascends much higher than the teeth back of it; thus the unworn tooth is much like a lance-shaped canine, much as in the Oligocene genus *Merycoidodon*.  $P_2$  is set very obliquely in the jaw, the external face is less convex than in *Merycoidodon*, and the tooth as a whole is very similar to that of *Ticholeptus zygomaticus*, viz., the crown is hypsodont; the internal face is divided into two simple and imperfect cavities by a heavy median ridge, which extends from the apex downward to the base; the anterior cavity is not bordered internally by a cingulum, while the posterior has a faint cingulum represented.  $P_3$  is larger than  $P_2$ , but is less oblique in the jaw. The external face is very similar to the preceding tooth, but the internal face is more unequally divided by a vertical ridge. As in the tooth preceding it, the anterior cavity has no internal cingulum, but the smaller posterior cavity is well margined. In the bottom of this posterior cavity is a thin, sharp ridge in the fore-and-aft direction, which subdivides the posterior cavity. In  $P_4$  the posterior cavity is completely surrounded, the internal crescent being fully developed, forming a complete connection posteriorly and anteriorly. The premolars are on the whole more hypsodont and narrower than those in *Merycoidodon*.

The molars are not unlike those in *Merycoidodon*, though more hypsodont and narrower. The comparatively long and narrow  $M_3$  of *Merychius* is a well marked feature in the present genus.

## MEASUREMENTS INFERIOR DENTITION.

	Paratype No. 1335
Antero-posterior diameter of inferior cheek dentition.....	90 mm.
Antero-posterior diameter of premolars.....	38 mm.
Antero-posterior diameter of molars.....	51 mm.
Antero-posterior diameter of $P_1$ at base of crown.....	11 mm.
Transverse diameter of $P_1$ at base of crown.....	5 mm.
Antero-posterior diameter of $P_2$ at base of crown.....	10 mm.
Transverse diameter of $P_2$ at base of crown.....	5 mm.
Antero-posterior diameter of $P_3$ at base of crown.....	12 mm.
Transverse diameter of $P_3$ at base of crown.....	5 mm.
Antero-posterior diameter of $P_4$ at base of crown.....	14 mm.
Transverse diameter of $P_4$ at base of crown.....	9 mm.
Antero-posterior diameter of $M_1$ at base of crown.....	13 mm.
Transverse diameter of $M_1$ at base of crown.....	9 mm.
Antero-posterior diameter of $M_2$ at base of crown.....	22 mm.
Transverse diameter of $M_2$ at base of crown.....	11 mm.
Antero-posterior diameter of $M_3$ at base of crown.....	24 mm.
Transverse diameter of $M_3$ opposite anterior crescent.....	12 mm.

*The Vertebral Column.* (Plates XVI-XIX.)—As previously stated the vertebral column of the type No. 1263 was found in position with all the vertebræ interlocked with one another, from the condyle of the skull to the sacrum; the latter is represented by the pleurapophysis of the first sacral, and there are four anterior caudals represented. In No. 1265 the sacrum is imperfectly preserved, and the tail is represented by seven or eight vertebræ next to the sacrum. With the exception of the sacrum and the caudal region we have thus an exact knowledge of the vertebral formula of this genus which may be stated as follows: seven cervicals, fourteen dorsals, six lumbar, ?five sacral, and eight + ?caudals.

*Atlas.* (Pl. XVI, figs. 1, 8, 9.)—In comparing the atlas with that of the well-known genus *Merycoïdodon* it is seen that the expanse of the transverse process in the present genus is proportionally smaller, and also that the arterial foramen near the posterior margin on the ventral face of the base of the transverse process is absent. This foramen is apparently quite normal in both *Merycoïdodon* and *Mesoreodon*, here used for comparison.<sup>7</sup> The atlas is incomplete in the skeleton of *Leptauchenia* here used for comparison, but from Dr. Sinclair's paper (Proceedings Amer. Philos. Soc., Vol. XLIX, 1910, fig. 1, pp. 197 and 199) it appears that the atlas differs from that of the present genus by a greater development of the dorsal arch and by the presence of the canal for the vertebral artery which perforates the base of the transverse process.

Professor Scott has stated (The Mammals of the Deep River Beds, p. 133) that the atlas of *Mesoreodon* "is rather more like that of the true ruminants than is that of *Eporeodon*." The present genus has the width of the transverse process even more uniform than in *Mesoreodon* and the posterior termination of the process is more prominent than in the latter genus. The vertical diameter of the atlas is very nearly the same as in *Merycoïdodon culbertsoni* (due partly to crushing) while the transverse is much less than in that species. The cotyli for the occipital condyle are well rounded, deep, greatly emarginated above, and less deeply separated at their inferior borders than in *Merycoïdodon*. The neural spine is quite rugose and proportionally as prominent as in the latter genus. Again, the vertical diameter of the articulation for the axis is greater, while the transverse is less than that of the older type. The neural canal is well proportioned in size, as are also the canals for the vessels.

*The Axis.* (Pl. XVI, fig. 2.)—The axis is on the whole more nearly like that of *Merychius* than *Merycoïdodon*. The neural spine and the body is, however, like

<sup>7</sup>The absence and presence of this arterial foramen is apparently varied in these genera since both Wortman (Bull. Amer. Mus. Nat. Hist. Vol. VII, 1895, p. 149) and Scott (Trans. Amer. Philos. Soc., Vol. XVII, 1893, p. 133) state that it is absent in the material which they studied.

that of the latter genus, but the cephalic articular surface has a greater vertical diameter, the odontoid process is broader, more depressed, and more distinctly spout-shaped, and there is no median rounded ridge on the superior face of the odontoid process and centrum as in *Merycoidodon*. The anterior exit of the vertebrarterial canal has a tendency to become bridged over as in *Merychys* and also in the recent peccary; this feature of the present genus is relatively that which obtains in *Promerycochærus carrikeri*, and apparently shows another mark of progress in modification from earlier types. The posterior perforation is smaller than in *Merycoidodon*. The inferior keel is quite prominent and terminates posteriorly in a rugose tubercle, which extends well back under the centrum of the succeeding vertebra, when in position in the neck. In *Leptauchenia* the body of the axis appears to be broader, the odontoid process less spout-shaped, and the transverse process heavier than in the present genus.

*The Third Cervical Vertebra.* (Pl. XVI, fig. 3.)—The chief characteristic difference of this vertebra from that of *Merycoidodon*, and apparently also of *Merychys*, is its proportionally longer neural arch. The tubercle on the inferior face of the centrum also projects downward to a greater degree and suggests that of *Leptauchenia* and also that of *Agriochærus guyotianus* (Bull. Amer. Mus. Nat. Hist., Vol. II, 1895, p. 150). The neural spine is broken off, but the fracture indicates a rather delicate spinous process, which was apparently less developed than in *Merycoidodon*. The zygapophyses are heavy, the posterior having a greater lateral expansion than the anterior, in order to meet the laterally expanded prezygapophyses of the succeeding vertebra. The transverse process has approximately the same relative strength as in *Merycoidodon culbertsoni* and is lighter than in *Leptauchenia*. The arterial canal is rather small.

*The Fourth Cervical Vertebra.* (Pl. XVI, fig. 4.)—This vertebra differs from the preceding only in minor detail. The transverse process is slightly heavier and the process on the inferior face of the centrum is more prominent than in the third cervical.

*The Fifth Cervical Vertebra.* (Pl. XVI, fig. 5.)—The transverse processes and the tubercle on the inferior face of the centrum of this vertebra are damaged; it can be seen, however, that the inferior keel and tubercle are smaller than in the preceding vertebra, a character also shown in the fifth cervical of *Leptauchenia*. The neural spine is also damaged, but the base indicates that the spine is robust and increases in size as in most genera of the family. The vertebrarterial canal pierces the pedicle at the base and is of rather small size.

*The Sixth Cervical Vertebra.* (Pl. XVI, fig. 6.)—The centrum of this vertebra

is more depressed than in the preceding vertebra; the inferior keel is feebly developed; the neural spine is quite robust, the pedicles are heavy, with a larger vertebrarterial canal than in the preceding vertebra; the pre- and postzygapophyses are heavy, and the inferior lamella of the transverse process droops greatly, and undoubtedly is hatchet-shaped in general outline, as is the case in most genera of the family.

*The Seventh Cervical Vertebra.* (Pl. XVI, fig. 7.)—The seventh cervical has the usual broad and depressed centrum and the high neural spine. The transverse process is quite heavy and outwardly projects horizontally and slightly forward; the pedicle is somewhat more compressed antero-posteriorly at the base, so as to cause a deeper intervertebral notch than in the preceding vertebra. There is no vertebrarterial canal. The cervical region as a whole is proportionally as heavy as in *Merychius*, and similar in details of structure.

*The First Dorsal Vertebra.* (Pl. XVI, fig. 10.)—This vertebra has the usual high and very robust neural spine; the spine is perhaps even higher than in *Merycoidodon*; and it is more attenuated and of greater antero-posterior diameter than in *Leptauchenia*. The centrum is depressed with a heavy and irregularly shaped keel. The anterior surface for the preceding vertebra is strongly convex and the capitular and tubercular facets for the first rib are separated only by a narrow and rather shallow groove on the base of the transverse process. The posterior face of the pedicle and the superior face of the centrum are quite deeply emarginated, forming a deep intervertebral notch, but the notch is not continued so far back on the anterior face of the transverse process as, for instance, in *Merycoidodon culbertsoni*. The postzygapophyses are less distinctly separated than in the latter species, and just above the facets, at the base of the neural spine, is a deep, round pit, which is similar to that in *Merychius*.

*The Second, Third, Fourth, Fifth, Sixth, and Seventh Dorsal Vertebrae.* (Pl. XVI, figs. 11 to 17.)—In receding order the centra of this series become less depressed vertically, more sharply and distinctly keeled, and the transverse processes decrease in length. The neural spines become gradually reduced in size and more backwardly inclined from the first to the last vertebra in this series. In *Leptauchenia* the neural spines have the antero-posterior diameter smaller. The proportionally greater vertical, and smaller transverse diameters of the centra in this series of dorsals, are striking characters, which differ from what is seen in *Merycoidodon*, in which the centra of the corresponding series are broader and vertically more depressed.

*The Eighth, Ninth, Tenth, and Eleventh Dorsal Vertebrae.* (Pl. XVI, figs. 17 to 21.)—This second series of dorsals has characters quite distinct from those of

the anterior series. The neural spines in these assume a more vertical position and have a greater antero-posterior diameter at their summits. The centra, however, continue high and narrow, as in *Promerycochærus carrikeri*, and unlike those in *Merycoïdodon culbertsoni*, which have the corresponding centra much depressed and expanded transversely, somewhat like those in the recent peccary. The transverse processes are higher up, and the ascending mammillary processes over the prezygapophysis gradually increase in length and prominence from the first to the last vertebra in this series. There are no distinct intervertebral foramina found on the sides of the pedicles.

*The Twelfth Dorsal Vertebra.* (Pl. XVI, fig. 21.)—This bone is chiefly characterized by having less perfectly interlocking prezygapophyses than is the case in *Merycoïdodon* and *Promerycochærus*. The postzygapophyses, on the other hand, have the articular surfaces rounded and similar in character to those of the lumbar series. The neural spine of this vertebra is more vertical than in those preceding it. The transverse process is located well forward on the side of the centrum and has an articular surface for the tuberculum of the rib, as in *Promerycochærus carrikeri* and as in the eleventh dorsal in *Merycoïdodon culbertsoni*. The centrum is high, narrow, and more gradually tapering downward, and consequently presents a sharper and more prominent keel than in *Merycoïdodon*.

*The Thirteenth Dorsal Vertebra.* (Pl. XVI, fig. 22.)—The neural spine of this vertebra has the true anticlinal position, while the spine of the vertebra preceding it is more nearly vertical. The transverse process is also less developed and there is no facet for the tubercle of the rib.

*The Fourteenth Dorsal Vertebra.* (Pl. XVI, fig. 23.)—On the left side of the centrum of this vertebra is preserved a facet, which definitely indicates that the bone supported a small rib. Furthermore, there were found fourteen ribs on each side in very nearly their relative positions and more or less complete, leaving no doubt that we are here dealing with the last thoracic vertebra<sup>8</sup>.

The centrum is high, narrow, and sharply keeled. The transverse process is quite well developed and occupies a median antero-posterior position on the upper part of the side of the centrum. The neural spine is broad antero-posteriorly, much compressed laterally and the pre- and postzygapophyses have a lumbar pattern. The vertebra as a whole is quite suggestive of the corresponding bone in *Leptauchenia*. It is also similar to the corresponding vertebra in *Promerycochærus carrikeri*, but with the keel less produced.

<sup>8</sup>In the skeleton of *Leptauchenia decora* at Princeton (No. 10773) here used for comparison, there are fourteen dorsal vertebræ. From Sinclair's studies (*l.c.* p. 198) this fact is already known.

*The First Lumbar Vertebra* (Pl. XVI, fig. 24.)—The transverse process of this vertebra suddenly increases in size, the antero-posterior diameter being twice that of the bone preceding it; the free end is also broader and more attenuated; there are otherwise only very few differences between the two bones.

*The Second, Third, Fourth, and Fifth Lumbar Vertebrae.* (Pl. XVI, figs. 25 to 28.)—This series of lumbar vertebrae are so similar to one another that a description for each one is not regarded as necessary.

The centra, when compared with those in *Merycoidodon culbertsoni*, are high and narrow, the transverse processes relatively somewhat shorter, and the neural spines less forwardly inclined. In *Phenacocælus typus* the transverse processes in receding order gradually increase in their antero-posterior diameter. The greatest antero-posterior diameter of the centrum appears in the fourth lumbar; the neural spine, which is wanting in the material examined, may also be in this vertebra the largest. Posteriorly, at the base, the neural spine of the fifth lumbar vertebra is less compressed transversely than in the preceding vertebra. In *Leptauchenia* the centra are somewhat more depressed, the transverse processes longer and more compressed fore-and-aft than in *Phenacocælus*, while the neural spines are similar in the two genera.

*The Sixth Lumbar Vertebra.* (Pl. XVI, fig. 28.)—The centrum is more depressed and shorter than in the preceding vertebrae, but in comparison with that of *Merycoidodon* it is high, and is more nearly like the centrum in *Merychius*. The transverse process is shorter and the antero-posterior diameter of the neural spine less than in the vertebrae in advance of it. The left transverse process and postzygapophysis are wanting, but on the right side the lamina bearing the postzygapophysis of the first sacral vertebra was found in position in the rock, so that the number of lumbar vertebrae in this specimen is regarded as correct. (See Pl. XVI, fig. 35).

*The Sacrum.* (Pl. XVI, fig. 35.)—Unfortunately in the type the sacrum is represented only by the right pleurapophyses and part of the prezygapophysial process of the first sacral vertebra. From the imperfectly preserved sacrum of No. 1265 it is possible to determine that the ilium is supported almost entirely by the pleurapophyses of the first sacral as in *Merychius*. There were probably five or six sacral vertebrae as in *Leptauchenia*.

*The Caudal Vertebrae.* (Pl. XVI, fig. 30.)—As indicated by the proximal eight caudals of the type, the tail, though of considerable length, was apparently not as long as in *Merycoidodon*. The neural arch soon disappears, the third caudal al-

ready having an imperfect canal, and the zygapophyses and neural spines are of rather small development. The transverse processes of the present series are, however, quite prominent.

## MEASUREMENTS

Length of vertebral column from condyles of skull to sacrum, all curves of the column included.....	605 mm.
Cervical region, length.....	125 mm.
Dorsal region, length.....	305 mm.
Lumbar region, length.....	160 mm.
Atlas; antero-posterior diameter.....	33 mm.
Atlas; transverse diameter.....	56 mm.
Atlas, transverse diameter of condylar articulation.....	31 mm.
Atlas, vertical diameter of condylar articulation.....	17 mm.
Atlas, greatest vertical diameter.....	28 mm.
Axis, greatest vertical diameter.....	44 mm.
Axis, transverse diameter of transverse processes.....	32 mm.
Axis, antero-posterior diameter of centrum, odontoid process included.....	36 mm.
Axis, length of odontoid process.....	11 mm.
Axis, vertical diameter, hypapophysis included.....	15 mm.
Axis, transverse diameter of centrum, posterior measurement.....	14 mm.
Axis, transverse diameter at articulation for atlas.....	30 mm.
Fourth cervical; antero-posterior diameter of centrum.....	21 mm.
Fourth cervical; vertical diameter of centrum, hypapophysis included.....	19 mm.
Fourth cervical; vertical diameter of hypapophysis.....	9 mm.
Fourth cervical; transverse diameter across transverse processes.....	30 mm.
Fourth cervical; transverse diameter of centrum, posteriorly.....	13 mm.
Seventh cervical; antero-posterior diameter of centrum.....	18 mm.
Seventh cervical; transverse diameter of centrum posteriorly.....	18 mm.
Seventh cervical; vertical diameter of centrum, posteriorly.....	11 mm.
First dorsal; antero-posterior diameter of centrum.....	18 mm.
First dorsal; transverse diameter at transverse processes.....	38 mm.
First dorsal; transverse diameter of centrum, posteriorly.....	22 mm.
First dorsal; greatest height in its position in the skeleton, approximately.....	75 mm.
Eighth dorsal; antero-posterior diameter of centrum.....	20 mm.
Eighth dorsal; transverse diameter of centrum posteriorly.....	12 mm.
Eighth dorsal; greatest height in its position in the skeleton.....	52 mm.
Fourteenth dorsal; antero-posterior diameter of centrum.....	23 mm.
Fourteenth dorsal; transverse diameter of centrum, posteriorly.....	12 mm.
Fourteenth dorsal; vertical diameter of centrum posteriorly.....	12 mm.
Fourteenth dorsal; greatest height in its position in the skeleton.....	40 mm.
Third lumbar; antero-posterior diameter of centrum.....	27 mm.
Third lumbar; transverse diameter at transverse processes.....	50 mm.
Third lumbar; transverse diameter of centrum, posteriorly.....	17 mm.
Third lumbar; vertical diameter of centrum, posteriorly.....	13 mm.
Third lumbar; greatest height in its position in the skeleton.....	39 mm.



## THE RIBS.

As stated above, there are twenty-eight ribs (fourteen on either side) represented in the type of this genus. Those in front are quite heavy and flattened; they are more expanded at the costal facet than in *Merycoiodon culbertsoni*. The tubercular and capitular facets are close together and the shaft of the rib has approximately the same curvature as in the latter genus. In the mid-dorsal region the ribs are less flattened, and further back they rapidly decrease in size, the thirteenth and fourteenth lacking the tubercular facets. The sternum is not present in the type and there are no sternobræ represented in the material at hand.

## THE SCAPULA, HUMERUS, RADIUS, ULNA.

*The Scapula.* (Pl. XVI, fig. 32.)—Both scapulæ are present in the type. The feeble development of the metacromion on the spine of the scapula in the present genus is an interesting feature. The area from the angle of the metacromion as far as the middle of the spine is rather broad and rugose, but there is no distinct metacromion process, such as is seen in *Merycoiodon culbertsoni* and in *Pro-merycochærus carrikeri*. This lack of a metacromion reveals a significant approach toward the condition in later selenodont artiodactyls and does not point especially toward an aquatic habit. In the recent peccary the thickened border, representing the metacromion, is nearer the suprascapular border than the glenoid cavity. In the present form the direction of the acromion process (*i. e.*, downward and forward) is quite similar to that in *Merycoiodon*, while further up the spine is less curved and slightly overhangs the postscapular fossa. The latter fossa is deeper and a trifle larger than the one in front of the spine. The glenoid border is very heavy and everted, so as to add to the depth of the postscapular fossa; above it terminates in a small and oblong tuberosity at the posterior angle. The coracoid is quite small and terminates in an obtuse hook-like process at the internal face of the head. There is a decided neck, while the blade again expands above, so that the infra- and post-spinous fossæ are of very nearly equal width at the vertebral border. The antero-posterior diameter of the glenoid cavity is approximately the same, while the transverse diameter is less than in *Merycoiodon culbertsoni*, thus presenting a more oblong articulation in the present genus. The sub-scapular fossa is comparatively small. The scapula of *Leptauchenia* is shorter and broader than in *Phenacocælus*, but otherwise this bone in the two genera is very similar.

*The Humerus.* (Pl. XVI, fig. 33.)—The right humerus is quite completely preserved in the type. In correspondence with the oblong glenoid cavity on the

scapula the articulating surface of the head of the humerus has a somewhat greater antero-posterior than lateral diameter, and it is less convex than in *Merycoiododon*. The greater tuberosity is relatively larger, especially in the antero-posterior direction, but rises less above the articulation of the head, while its extent across the entire anterior face is similar to that in *Merycoiododon*. Part of the lesser tuberosity is damaged, but it can be determined that it is relatively as robust and as large as in *Merycoiododon*. The bicipital groove is of moderate size and is apparently more open above than in *Merycoiododon culbertsoni* and *Promerycochærus carrikeri*. On a direct front view the shaft presents a sigmoid curve, which has, to a small extent, been caused by crushing. The deltoid ridge is quite prominent, more so than in *Merycoiododon*. The shaft, though much shorter, is very nearly as heavy and rounded as in *Merycoiododon culbertsoni*.

The distal trochlea is characterized by the same obliquity as in *Promerycochærus carrikeri*. Unfortunately the inner face of the internal condyle is broken off, but, judging from the very broad inter-condylar ridge, the transverse expanse of the distal end must have been considerable. The external trochlea is relatively somewhat smaller than in *Promerycochærus carrikeri* and much smaller than in *Merycoiododon culbertsoni*. This is a marked advance towards the condition found in the recent Artiodactyla. The small part of the internal epicondyle, which is present, indicates that it had perhaps very nearly the same relative size as in *Merycoiododon*. The anconeal fossa is high and rather narrow, the external border overhanging the fossa more than is seen in the latter genus and in *Promerycochærus*. There is a perforation of the thin wall of this fossa, which may, or may not, be a true supratrochlear foramen. The supinator ridge is only moderately prominent.

In *Leptauchenia* the humerus is of the same proportionate length as in the genus under description, but the bicipital groove is larger, the proximal end of the shaft heavier, the portion above the supinator ridge slenderer, and the trochlea and distal end broader.

*The Radius.* (Pl. XVI, fig 34; Pl. XIX.)—The radius is characteristically merycoiodont; thus the broad head and round shaft are at once recognizable features. The external division of the humeral facet of the radius is much reduced, the ridge separating it from the median region is less prominent, while the median and internal facets are proportionally larger than in *Merycoiododon*. This is quite in keeping with conditions found on the distal trochlea of the humerus. The radius shows no indication of coalescence with the ulna, but the head is articulated more firmly with the anterior face of the ulna than in *Merycoiododon*. The broad transverse surface of the head rapidly decreases downwardly, so that the shaft

very soon becomes quite rounded, even more so than is observed in Oreodonts generally. More distally the shaft again arches more backward and is flatter transversely.

The distal end of the radius is more strongly flexed outward than in *Merycoidodon*, so that the manus, when in position, points outward rather unusually. The transverse and antero-posterior expansion are very nearly as great as in *Merycoidodon culbertsoni*. The anterior face is well marked by the broad groove for the extensor tendon. The distal articular facets are injured, especially the one for the scaphoid; however, enough is preserved to indicate the great obliquity of this facet as in the larger Oreodonts (*Promerycochærus montanus*, *P. carrikeri*, and *Merycochærus*) and also to show that the facet was flexed quite high on the radial posterior angle. The lunar facet is of relatively greater transverse diameter than that in *Merycoidodon*, and it has a higher position on the bone than is seen in the latter genus.

The proximal end of the radius in *Leptauchenia* is more suddenly expanded transversely than in *Phenacocælus*. The shaft has a greater forward bow and the distal end has a proportionally greater antero-posterior and less transverse diameter than in the latter genus. The oblique position of the facets for the carpus in *Leptauchenia* is especially similar to that of *Phenacocælus* described above.

*The Ulna.* (Pl. XVI, fig. 34; Pl. XIX.)—The ulna is not reduced and is even comparatively more robust than in *Merycoidodon culbertsoni*. The upper end of the olecranon process was found incomplete, but what remains indicates that it was as heavy as in the Oreodonts generally. In correspondence with the narrow antconeal fossa of the humerus the upper humeral articulation of the sigmoid cavity is small in transverse diameter, when compared with *Merycoidodon*, while the lower portion of the cavity is actually broader than in the latter genus. The internal angle of the humeral articular surface is well developed and extends nearly even with the internal face of the head of the radius. Externally there is a broad facet for the head of the radius. This facet is bounded externally by a very prominent ridge, which continues downward, as the antero-external border of the shaft, and is much more prominent than in *Merycoidodon*. The shaft of the ulna presents a trihedral section in the upper portion, while lower down it is more nearly flat; it is much arched in order to accommodate itself to the curve of the shaft of the radius. Postero-radially is a prominent ridge, which extends from near the distal end one-third up on the shaft and overlaps the posterior face of the shaft of the radius, as in *Promerycochærus carrikeri*. This feature is far more prominent than in *Merycoidodon*. The cuneiform facet has a relatively greater transverse, but somewhat

less antero-posterior diameter, than in the latter genus. Furthermore, the facet is more convex antero-posteriorly and extends higher up upon the bone in front and behind; the pisiform articulation is consequently quite continuous with that for the cuneiform.

The distinguishing feature of most prominence in the ulna of *Leptauchenia* is the great development of the tubercle for the attachment of the internal humeral part of the triceps muscle. This tubercle, located on the antero-internal angle of the upper end of the olecranon process, is proportionally much more developed than in *Phenacocælus* and greater than in any genus of the family known to the writer, *Agriochærus latifrons* from the Oligocene included. In size the ulna of *Leptauchenia* is fully as large, if not larger, proportionally than in *Phenacocælus*. The distal portion of its shaft does not overlap the posterior face of the shaft of the radius as in *Phenacocælus*, as already described.

#### THE CARPUS.

The carpus is actually higher than in *Merycoïdodon* and very nearly as broad; otherwise the structure of this region bears a close similarity to the latter genus, with which it is herewith compared.

*Scaphoid.* (Pl. XVII, figs. 5, 6.)—The scaphoid is higher than in *Merycoïdodon*, its transverse diameter smaller dorsally, while on the palmar side it is broader. The articulation for the radius is more convex anteriorly and rises more rapidly on the ulnar side,<sup>9</sup> but the posterior part of the articulation is less strongly concave antero-posteriorly. This is due to the less elevated palmar protuberance in *Phenacocælus*. This palmar protuberance is produced rather more radially in the latter form, so that the palmar face is proportionally and actually broader than in *Merycoïdodon*. On the ulnar side the bone in the type is more deeply excavated, and overhangs above more in the ulnar direction, so that the superior ulnar angle of the bone reaches over and forms a contact with a corresponding face on the radial side of the lunar.\* The inferior articulation for the lunar is of greater vertical extent than in *Merycoïdodon*, but, as in the latter, it continues quite to the palmar face of the scaphoid. The distal surface is unevenly divided by a well-defined ridge, which extends antero-posteriorly and separates the larger facet for the magnum from the smaller facet for the trapezoid. Both facets are concave antero-posteriorly.

The scaphoid of the specimen of *Leptauchenia* at Princeton (No. 15757) is incomplete. It is possible, however, to ascertain from the fragment that the facet

<sup>9</sup>The elevation on the ulnar angle is variable.

for the radius did not extend downward so much on the dorsal face as in *Phenacocælus*, while in the palmar radial region there is a more rapid elevation of this facet, due to the greater elevation of the palmar protuberance in this region. The facets for the magnum and the trapezoid are more nearly subequal in size and separated by a ridge of greater prominence than in *Phenacocælus*.

*Lunar.* (Pl. XVII, figs. 5, 6.)—The lunar is higher than in *Merycoidodon culbertsoni*. Proximally the facet for the radius is deflected lower down on the anterior face of the bone, so that the articulation is more obliquely convex fore-and-aft than in the latter genus. On the anterior face of the lunar there is a horizontal and rugose ridge at the termination of the deflexed articular facet for the radius, which extends quite across the anterior face of the bone, causing the dorsal surface below this band to be concave vertically. Radially the lunar is much excavated and the facet for the scaphoid is less distinctly separated from that of the magnum than is seen in *Merycoidodon*; it is also quite strongly convex antero-posteriorly, and the beak of the lunar reaches well down, but does not come in contact with the head of the third metacarpal. On the ulnar side the bone is excavated deeply, but the prominent elevated lip, near the proximal face of the lunar in *Merycoidodon*, is much less prominent and less overhanging in *Phenacocælus*; the cuneiform facet is also more restricted to the anterior portion of the bone. Distally the lunar is, as in *Merycoidodon*, almost entirely taken up by the somewhat obliquely placed facet for the unciform. The bone has a much smaller transverse diameter posteriorly than in *Merycoidodon*.

The lunar of *Leptauchenia* is broader and lower than in *Phenacocælus*. The facet for the radius is narrower, less convex antero-posteriorly, and has a more oblique position than in *Phenacocælus*. Distally the beak-like process is shorter and placed further from the radial face of the bone than in the genus under description, but the bone rests almost entirely on the unciform as in the latter genus.

*Cuneiform.* (Pl. XVII, figs. 5, 6.)—The cuneiform is quite characteristic. All its diameters, except the antero-posterior, are greater than in *Merycoidodon*. The articular surface for the ulna is more deeply set, the anterior border of the articulation being higher than in the latter form and more closely approaching the condition found in the recent peccary. The anterior face of the cuneiform is less convex than in *Merycoidodon culbertsoni*; and on the radial face there is a deeper excavation above the lunar facet. The latter facet is more convex and higher near the anterior face, then gradually decreases in height posteriorly, while the facet in *Merycoidodon* is slightly convex antero-posteriorly and is as high behind as in front. On the ulnar side the cuneiform greatly overhangs the unciform, even more

so than in *Merycoïdodon*. The posterior face is an unevenly convex and rugose surface. The facet for the pisiform is not so close to the ulnar angle of the bone as in the latter genus. On the distal surface the bone has a large cup-shaped facet for the unciform.

In *Leptauchenia* the cuneiform is relatively broader and shallower than in *Phenacocœlus*. The articulation for the ulna is quite similar to that in the latter genus, while that for the pisiform is proportionally larger. The articulation for the unciform is also less cup-shaped than in *Phenacocœlus*.

*Pisiform*. (Pl. XVII, fig. 5, 6.)—The pisiform, though similarly constructed, is much more delicate than in *Merycoïdodon*. The vertical diameter is somewhat greater, while transversely it is much more attenuated, and its entire length is also less than in that genus.

The pisiform of *Leptauchenia* is proportionally somewhat slenderer than in *Phenacocœlus*, but otherwise the bone is similarly constructed in the two genera.

*Unciform*. (Pl. XVII, figs. 5, 6.)—The general outline of the unciform is very similar to that in *Merycoïdodon*, but a closer examination reveals a number of characteristic differences. The bone in the present genus has comparatively greater vertical and smaller transverse diameter. The proximal surface of the unciform, which supports the lunar and cuneiform, has an unusually even convexity, showing little or no separation between the two facets. On the postero-radial angle of the lunar articulation is a small round facet, which articulates with a corresponding facet on the end of a projecting arm on the ulnar side of the magnum; this is the only point of contact between the latter bone and the unciform. On the anterior face the unciform is slightly convex in all directions, and near the proximal angle is a narrow groove, which extends across nearly the entire width of the bone. Radially the unciform is partly taken up by the articular surface for Mc. III, which is succeeded by a deep excavation further back. The articular facets for the fourth and fifth metacarpals are divided by a prominent ridge directed antero-posteriorly. The latter facets are concave antero-posteriorly, the two facets together forming a saddle-shaped appearance. The facet for the fourth metacarpal has a proportionally smaller transverse diameter than in *Merycoïdodon*.

The unciform of *Leptauchenia* available for comparison is not entirely complete, but it is easily determined that the bone is proportionally broader, lower, and the palmar hook shorter than in *Phenacocœlus*.

*Magnum*. (Pl. XVII, figs. 5, 6.)—The magnum is proportionally smaller than in *Merycoïdodon culbertsoni*. The chief characteristic difference from that of the latter genus is the greater vertical ulnar face of the bone. The lunar facet in the

present genus is less oblique and does not extend over the top of the posterior convex surface as in *Merycoïdodon*, but articulates with the lunar laterally. The facet for the scaphoid is the only articulation, which is entirely proximal in the type specimen, and it is much convex antero-posteriorly, with an oblique downward slope from the ulnar to the radial side. Radially the magnum is deeply emarginated for the contact with the trapezoid. The small anterior face is slightly convex and rugose. Distally the bone has one large saddle-shaped facet for the third metacarpal. The palmar hook is less prominent than in *Merycoïdodon*, but in the type there is present the characteristic articulation on the ulnar side for a corresponding facet on the postero-radial side of the palmar process of Mc. III. In other individuals the latter character is less noticeable, or entirely wanting in the present genus.

*Trapezoid.* (Pl. XVII, figs. 5, 6.)—The trapezoid is an irregular nodular bone, which articulates with the magnum, as in *Merycoïdodon*; and, as in that genus, the distal end is almost entirely taken up by the articular facet for Mc. II. The small round facet for the trapezium is located well down on the posterior face of the bone. As a whole the trapezoid is approximately of the same relative size as in *Merycoïdodon*.

*Trapezium.* (Pl. XVII, figs. 5, 6.)—The trapezium is also of the same relative size as in *Merycoïdodon*, but there is no facet for the first digit. On the other hand there appears to be a small rounded facet on the ulnar side, which articulates with the postero-radial face of the head of Mc. II.

The magnum, trapezoid, and trapezium are not present in the material of *Leptauchenia* from Princeton here used for comparison.

#### THE METACARPALS AND PHALANGES.

There is no evidence of a pollex in the manus of *Phenacocælus*. The end of the second metacarpal is wanting, as is also that of the fifth. The chief differences between the metacarpals of the present genus and *Merycoïdodon* are: the more robust, though perhaps somewhat shorter, Mc. V; and the general broadness and more flattened condition of the metacarpals in *Phenacocælus*. The length of Mc. III and Mc. IV is approximately the same as in *Merycoïdodon*; the distal ends are rounded in a similar manner; and the articular surfaces for the carpals are similar.

There are no phalanges of the manus preserved in the type, but from the paratypes it is observed that these bones are depressed as in *Merycoïdodon*, and are also fully as long or even longer than in that genus. The terminal phalanges are somewhat more depressed and broader than in *Merycoïdodon*.

The metacarpals and phalanges of *Leptauchenia* are incompletely represented

in the material from Princeton here used. However, it is clear that the shafts of the metacarpals appear to be broad and flat, as in *Phenacocælus*. The phalanges of the proximal and median rows are also depressed and broad as in the latter genus, while the unguals in *Leptauchenia* are poorly represented, the only one present being of a lateral digit, and appears to be pointed, high, and rather narrow. From Dr. Sinclair's study of *Leptauchenia* (*l. c.* p. 197, fig. 1) it would appear that the metacarpals are shorter than the metatarsals approximately in the same proportion as in *Merycoïdodon*.

MEASUREMENTS OF FORE LIMB.	Type No. 1263
Scapula, height.....	106 mm.
Scapula, antero-posterior diameter at vertebral border.....	75 mm.
Scapula, antero-posterior diameter of glenoid cavity including coracoid.....	24 mm.
Scapula, transverse diameter of glenoid cavity.....	15 mm.
Scapula, greatest depth of spine.....	19 mm.
Humerus, greatest length.....	137 mm.
Humerus, antero-posterior diameter of head.....	37 mm.
Humerus, transverse diameter of head.....	29 mm.
Humerus, transverse diameter of distal end, approximately.....	27 mm.
Humerus, antero-posterior diameter of distal end.....	21 mm.
Radius, greatest length.....	109 mm.
Radius, transverse diameter of head.....	20 mm.
Radius, antero-posterior diameter of head.....	10 mm.
Radius, antero-posterior diameter of distal end.....	10 mm.
Radius, transverse diameter of distal end.....	19 mm.
Ulna, greatest length, approximately.....	140 mm.
Ulna, transverse diameter of sigmoid cavity, inferior part.....	20 mm.
Ulna, transverse diameter of distal end.....	11 mm.
Ulna, greatest antero-posterior diameter of distal trochlea.....	4 mm.
Carpus, height, at ulnar angle.....	20 mm.
Carpus, breadth, proximal row of bones.....	26 mm.
Pisiform, total length.....	18 mm.
Metacarpal III, length.....	53 mm.
Metacarpal IV, length.....	52 mm.

#### THE HIND LIMB.

*Pelvis.* (Pl. XVI, fig. 36.)—The right ilium and the anterior part of the ischium are the only parts of the pelvis preserved in the type specimen. The chief point of difference between *Merycoïdodon culbertsoni* and *Phenacocælus* at this point is the much heavier and more rugose acetabular border in the latter. The border above the sacro-iliac contact of the ilium is broken off, but on the whole the vertical diameter of the ilium seems to have been somewhat less than in *Merycoïdodon*. The fragment of the ischium indicates similarities to the corresponding part in *Merycoïdodon*. The acetabulum is partly destroyed, but it is possible to ascertain



that it is quite deep and that the anterior border is heavy and slightly curved backwards, so as to more completely lock the head of the femur than is the case in *Merycoidodon*, and is in this respect more like what is found in *Merychius*. Only a part of the cotyloid notch is preserved, which is in all respects similar to that in *Merycoidodon*. From one of the paratypes (No. 1265), it is possible to determine that the pelvis is broad posteriorly, forming a broad pelvic cavity as in *Merychius*. The outline of the obturator foramen in this specimen is also present; it shows that this foramen is of the usual size and proportions, and oblong in shape. The ascending process of the pubis is short, though quite robust, and the horizontal ramus was apparently broad transversely.

In *Leptauchenia* the pelvic girdle is proportionally as heavy or possibly even heavier than in the genus under discussion. The transverse expansion, especially along the ventral borders of the ilia, is greater and the pelvic cavity is also apparently fully as great or greater than in *Phenacocælus*, while the ischium and ilium together form a bar of bone more nearly straight in the fore-and-aft direction than in the latter genus. This is due to the smaller prominence of the spine of the ischium and to the less expanse of the ilium in the dorsal direction in *Leptauchenia*.

*Femur*.—It is unfortunate that the femur of the type is represented only by a short section of the shaft, which gives no character worthy of note, beyond the fact that the circumference is similar to that in specimens provisionally referred to another species of this genus, which will be described later. It may be provisionally said that the femur appears to be relatively longer than in *Merycoidodon* and *Leptauchenia*. There is no patella preserved with the type specimen.

*Tibia*. (Pl. XVII, figs. 37-39.)—The extreme proximal end of the tibia is broken off, otherwise the bone is complete. The shin-bone is, however, proportionately stouter than that of *Merycoidodon* and also differs from that of *Merychius minimus* from the Upper Harrison beds. The cnemial crest is very prominent and overhangs the fibular side of the shaft to a greater degree than in both *Merycoidodon* and *Merychius*, and the anterior face of the shaft, below the crest, continues more prominently to the distal end, so that the shaft has a marked obliquity in the postero-fibular direction not seen in the other genera mentioned. The posterior, the tibial, and the fibular faces of the shaft are not unlike what is seen in *Merycoidodon*. Distally, however, the tibia has a greater transverse diameter. The internal malleolus, though somewhat shorter than in *Merycoidodon*, is fully as robust, and has the usually everted free end for a more completely locked ankle-joint; a common feature seen in this family. The trochlea displays the usual oreodont features, viz, the narrow and low external groove, the broader and

much higher located internal groove. The tibial face of the distal end is slightly damaged.

*Fibula.* (Pl. XVI, figs. 37-39.)—The shaft of the fibula appears proportionally as heavy as that of *Merycoïdodon*. The distal end is, as usual, enlarged, quite rugose, and with a deep excavation on the tibial face for contact with a well formed facet for the calcaneum.

In *Leptauchenia* the tibia is much more delicate in its general proportions than in *Phenacocælus*. The bone is also relatively longer than in the latter. The cnemial crest does not extend so low, the median region of the shaft is more nearly cylindrical, and the fibular face of the distal end is less excavated for the reception of the fibula. The latter is proportionally slenderer than in *Phenacocælus*.

#### THE TARSUS, METATARSALS, AND PHALANGES.

One of the most significant characteristics of this genus is its broad and short hind foot. The pes is on the whole shorter than the manus, which is a feature differing not only from the *Agriochæridæ*, but from the *Artiodactyla* generally. In *Leptauchenia* the pes is longer than the manus in the usual proportion seen in the family *Agriochæridæ*.

*Calcaneum.* (Pl. XVII, figs. 9-10.)—The tuber of the calcaneum is short and heavy; the tendinal groove is oblique and rather shallow, while the facet for the astragalus on the lesser process is at a more direct right angle than in *Merycoïdodon*, so that, when the bone is in position, it throws the free end of the tuber towards the tibial side and the fibular face downward to a greater degree than is seen in the latter genus. The groove for the interosseous ligament is relatively smaller and the anterior face of the cuboid facet is broader than in *Merycoïdodon*.

In *Leptauchenia* the sustentacular facet is of relatively greater vertical diameter in order to conform to the higher astragalus, and the tuber is also more trihedral in cross-section than in *Phenacocælus*. Furthermore, when the bone is in position, it has apparently a more direct fore-and-aft position in *Leptauchenia* than in *Phenacocælus*.

*Astragalus.* (Pl. XVII, figs. 7-8.)—The astragalus is broader and lower than in *Merycoïdodon culbertsoni* and more nearly like that of *Merycochærus* from the Upper Harrison Beds. Some features of the astragalus also recall that of *Argiochærus major* (Bull. Am. Mus. Nat. Hist., Vol. VII, p. 168, 1895), viz., the great transverse diameter and short neck. The external condyle of the proximal trochlea differs from that of *Merycoïdodon culbertsoni* by being more oblique and higher. The external face also overhangs the calcaneal facet and the median groove is

crowded over more to the internal side, so as to cause an unusually small internal condyle. This condition of the external condyle is apparently due to the outwardly forced upper end of the astragalus. The neck, as above stated, is short, but distinctly separates the proximal and distal trochleæ. The facet for the malleolus of the tibia appears as an irregular and rather deep groove on the tibial face, which is chiefly due to a prominently developed knob near the proximal plantar angle. On the fibular plantar angle there is another large rounded excavation for the articulation with the calcaneum. The navicular portion of the distal trochlea is apparently not so deep as in *Merycoidodon* and more like that of *Merycochærus*, but, as in the latter genera, the navicular facet is much larger than the facet for the cuboid. The sustentacular facet is not so deep as in *Merycoidodon culbertsoni*, otherwise it is similar.

The astragalus of *Leptauchenia* has proportionally a greater vertical and smaller antero-posterior diameter than is the case in *Phenacocælus*. The facet for the cuboid is also more oblique and narrower than in the latter genus, but otherwise the bone is in general similar in the two genera.

*Cuboid.* (Pl. XVII, figs. 9-10.)—The cuboid has a broader anterior face than in *Merycoidodon*, which results in a more triangular articulation for the fourth metatarsal. The astragalar facet is extremely concave antero-posteriorly, and terminates in a high ascending border on the plantar angle. The articular surface for the calcaneum is broader anteriorly than in *Merycoidodon*, but holds practically the same angle of elevation before backward. The antero-posterior diameter of the bone is proportionally somewhat less than in *Merycoidodon*, while the plantar process is more alike in the two genera. The articular facet for the fifth metatarsal is distinctly separated from that for the fourth by a raised ridge, which is more prominent posteriorly and gradually fades away near the anterior margin; this facet is somewhat lateral on the posterior angle.

In *Leptauchenia* the cuboid is proportionally higher and the facet for the astragalus is comparatively even, more concave antero-posteriorly, and deeper than in *Phenacocælus*, but in other details the differences are not great.

*Navicular.* (Pl. XVII, figs. 9-10.)—The navicular is low and broad, the articular facet for the astragalus is subtriangular in outline with the apex backward, concave antero-posteriorly, and convex laterally, especially on the fibular side. On the distal face is an oblong flat articulation for the coössified ecto- and meso-cuneiforms. The tubercle on the tibial face is of the same proportion as in *Merycoidodon*, but the plantar hook-like process is flatter and is less produced downward than in the latter.

The palmar process of the navicular in *Leptauchenia* is relatively longer than in *Phenacocælus*, otherwise the bones of the two genera are not unlike.

*Ecto- and meso-cuneiform.* (Pl. XVII, figs. 9-10.)—The coössified ecto- and meso-cuneiform is not so triangular in outline as in *Merycoidodon*, which is due to the much smaller development of the plantar tubercle near the proximal face of the bone in the present species. In all other respects the compound bone is similar in the two genera. In *Leptauchenia* the ecto- meso-cuneiform is oblong, as in *Phenacocælus*.

*Ento-cuneiform.* The ento-cuneiform has a more triangular outline on cross-section than in *Merycoidodon culbertsoni*. The basin-shaped facet for the navicular, the facets on the external face for the compound cuneiforms and Mt. V on the nodular-shaped bone, are all closely similar to those in *Merycoidodon*. In *Leptauchenia* the ento-cuneiform is less triangular on cross-section than in *Phenacocælus*.

*Metatarsals.* (Pl. XVII, figs. 9-10.)—The metatarsals are unusually short and heavy; they are shorter and heavier than the metacarpals, which is a condition contrary to that usually found in the family, except in the genus *Agriochærus*. The second metatarsal is the shortest. The metatarsals increase in length in the following order: the fifth, third, and the fourth. *Agriochærus latifrons* is set up in an articulated position in the American Museum of Natural History and from the figure of the restoration (Bull. A. M. N. H., VII, 1895, Pl. 1) it seems to appear that the metatarsals are shorter than the metacarpals.<sup>10</sup>

The second metatarsal is considerably reduced in length, but otherwise this element is fully as robust as in *Merycoidodon*. The head rises slightly above the head of Mt. III, and there is a small facet for the meso-cuneiform on the proximal face. On the tibial face the bone articulates with Mt. III in the usual manner, and there is a rough surface on the antero-tibial angle of the head, behind which is located the rather large-sized articular facet for the ento-cuneiform. The shaft is more rounded than in any other metatarsal of the pes, but rapidly expands distally, especially on its tibial face, where a heavy and rugose ridge takes its origin near the distal articulation and continues well up upon the shaft. (See Pl. XVII, figs. 9-10). The carina is quite strongly developed, but, as in *Merycoidodon*, entirely confined to the plantar face of the articulation.

The second metatarsal of *Leptauchenia* is lighter and longer in proportion, and the distal tibial face has not the heavy and rugose ridge seen in *Phenacocælus*.

<sup>10</sup>Wortman states (*l.c.* p. 164) that the manus and pes are subequal in length.

The third metatarsal is reduced in length in the same proportion as in *Merycoïdodon*. Superiorly the bone is well interlocked by metatarsals II and IV and by the ecto-meso-cuneiforms. The shaft is rather flattened and more strongly arched than in *Merycoïdodon*, but distally the articular facet for the proximal phalanx has a less antero-posterior diameter than in the latter genus. The carina is fully as well developed, while dorsally the articular surface extends higher up than in *Merycoïdodon*.

Mt. III in *Leptauchenia* is quite similar to that of *Phenacocælus*, except in its greater proportionate length and in the dorsal portion of the articulating trochlea for the first phalanx, which does not extend as high as in *Phenacocælus*.

Metatarsal IV is the heaviest in the series. On the proximal end the anterior portion of the articulation for the cuboid is gently convex from side to side, while on the posterior part of the head there is a strong plantar tubercle, which shares the support for the cuboid to a somewhat greater extent than is seen in *Merycoïdodon*; this portion of the facet is more oblique and located higher than the portion in front. On the tibial face is a strong articular lip, which is well fitted into a corresponding pit on the fibular side of Mt. III, and an elongated facet posterior to this lip completes the interlocking condition of the articulation. On the fibular side the articulation for Mt. V is less complicated. The shaft is heavy and slightly more expanded distally than in *Merycoïdodon*. When in position in the pes the fourth metatarsal is seen to extend below the third in approximately the same proportion as in *Merycoïdodon*.

In *Leptauchenia* Mt. IV is proportionally longer than in *Phenacocælus*, but otherwise there are no noteworthy differences in this bone in the two genera.

Metatarsal V is fully as strongly developed as in *Merycoïdodon*. The proximal end is well fitted against Mt. IV on the tibial face, while above there is a small oblong facet for the cuboid. Distally there is a well formed articular facet for the proximal phalanx.

*Phalanges.* (Pl. XVII, figs. 9-10.)—The phalanges of the second digit are all present; those of the other digits are less completely preserved in the type. The phalanges, especially the outer series, are somewhat more depressed and more expanded laterally, than in *Merycoïdodon*.

In *Leptauchenia* there is possibly less difference between the length of the fifth and the second metatarsals than is the case in *Phenacocælus*. As before stated, the phalanges of *Leptauchenia* are very poorly represented, but they were possibly somewhat higher and narrower than in *Phenacocælus*.

MEASUREMENTS	Type No. 1263
Ilium, from anterior border of acetabulum to point of ilium.....	90 mm.
Ischium, vertical diameter at posterior part of acetabulum.....	29 mm.
Tibia, length approximately.....	112 mm.
Tibia, length of fragment preserved.....	105 mm.
Tibia, antero-posterior diameter of shaft at cnemial crest.....	29 mm.
Tibia, transverse diameter of shaft at cnemial crest, posterior measurement.....	14 mm.
Tibia, transverse diameter of distal trochlea.....	23 mm.
Tibia, antero-posterior diameter of distal trochlea.....	13 mm.
Calcaneum, greatest length.....	45 mm.
Calcaneum, antero-posterior diameter of cuboid facet.....	13 mm.
Calcaneum, transverse diameter of cuboid facet, anterior measurement.....	7 mm.
Astragalus, greatest height, approximately.....	24 mm.
Astragalus, greatest breadth.....	19 mm.
Cuboid, height, anterior measurement.....	10 mm.
Tarsus, transverse diameter.....	25 mm.
Metatarsal II, length.....	33 mm.
Metatarsal III, length.....	46 mm.
Metatarsal IV, length.....	48 mm.
Metatarsal V, length.....	37 mm.
Phalanges 2nd digit, length.....	37 mm.
Phalanges 3rd digit, length.....	45 mm.
Phalanx, terminal, 4th digit, length.....	15 mm.

#### NOTES ON COMPARISON OF PARATYPES WITH THE TYPE SPECIMEN OF PHENACOCÆLUS TYPUS PETERSON.

In the material discussed in the foregoing pages there are some marked variations worthy of brief notice. These variations might (possibly justly) by some students be regarded as of specific value, but, with one exception (No. 1288), hereafter described, I prefer to regard the differences as being individual and sexual.

On comparison of skull No. 1278 with all the rest of the material representing the head in the series before me I detect the following anatomical points, showing<sup>11</sup> that this specimen discloses: (1) a smaller tympanic bulla; (2) a smaller antero-posterior diameter of the postglenoid process; (3) a larger external auditory meatus, possibly located somewhat further back, and more like what is seen in *Leptauchenia*; (4) a general reduction in the relative length of the skull. With the exception of the first and third features noted, I think it is possible, in fact most probable, that the curious appearance of this specimen is due entirely to crushing. At all events I refrain from here establishing a species because of the excessive crushing of the skull. (See Pl. XVIII, figs. 12-13).

Specimen No. 1288 consists of the lower jaws, fragments of the atlas and other

<sup>11</sup>The skull in question is very much crushed antero-posteriorly.

cervicals, two anterior dorsals, a fragment of the sacrum, fragments of ribs, portions of both radii, and the manus fairly well preserved, the right side of the pelvis nearly complete, and a fragment of the left ilium, the right femur very nearly complete, and the head of the left, both tibiæ nearly complete, and the pes well represented. The material indicates an animal of slightly larger size than the type of *P. typus*.

After lengthy and minute comparison of this material (No. 1288 Carn. Mus. Cat. Vert. Foss.) I am finally constrained to designate it as the type of a new species of *Phenacocælus*. The description herewith follows:

***Phenacocælus munroënsis***<sup>12</sup> sp. nov.

(Pl. XVIII, figs.1-9)

The cheek-teeth of the lower jaw are somewhat more delicate than in the paratypes, Nos. 1278 and 1335 of *P. typus*, but this may well be a sexual difference, as the dentition is otherwise quite similar. The symphysial region of the lower jaws is less spout-shaped than in the paratypes referred to above, which may partly be due to crushing. The angle is, however, less flexed inwardly, and thus not quite like the condition found in *Leptauchenia*.

The fragments representing the vertebral column of the present specimen do not present any important differences from those in the type of *P. typus*, or in the material of other individuals. In the fore limb, on the other hand, there appear some very marked differences. It is possible to determine from the remains of the radii before me that No. 1288 has a longer and relatively slenderer shaft. Unfortunately the proximal end of both radii are not present, but what remains of the distal end of the shaft, especially of the left radius, it is seen to be very nearly as long as the entire bone in the type. The broken end of the shaft does not display the characteristic broadening immediately below the head, observed in a complete radius of *P. typus*. I feel certain, therefore, that the bone when complete must have been at least 30 mm. longer, which would give a length 15 to 20 mm. over that in the type of *P. typus*. As in the latter, the shaft of the radius is rod-like throughout, a feature more primitive than in *Merycoidodon*. With the exception of the slightly larger size of the specimen under description, there are no characters of importance by which the fore limb differs from the type or paratypes of *P. typus*.

In correspondence with the fore limb the hind limb is also found to be longer

<sup>12</sup>The specific name is based upon the geological locality, the Monroe Creek Beds, at the head of Warbonnet Creek, Sioux County, Nebraska, where the specimen was found.

and somewhat slenderer than in *P. typus*. No differences worthy of note are observed in the pelvis. The femur is long and slender, its head being placed rather more proximally, which to some extent is possibly due to crushing. There is an unusually deep trochanteric fossa and the lesser trochanter is also quite prominent. The shaft, as stated is slender, while the distal end is suddenly expanded both laterally and antero-posteriorly. There is no femur present with the type of *P. typus*. In the tibia, however, one is able to again observe a greater length, otherwise with little or no greater size of the bone. Again, while the tarsals are in general quite similar, the metatarsals are a trifle longer in No. 1288. In this specimen the metatarsals are seen to be very nearly as long as the metacarpals, while those of the type of *P. typus* as noted in the foregoing work, are considerably shorter than the metacarpals.

MEASUREMENTS	Type No. 1288
Mandible, length.....	150 mm.
Mandible, height at angle, including coronoid process.....	95 mm.
Mandible, depth at M <sup>3</sup> .....	45 mm.
Mandible, depth at P <sup>3</sup> .....	23 mm.
Mandible, length of dentition.....	103 mm.
Mandible, length of molar series.....	50 mm.
Mandible, length of premolar series.....	40 mm.
Radius, length of fragment.....	100 mm.
Carpus, height.....	21 mm.
Metacarpal III, length.....	60 mm.
Metacarpal IV, length.....	58 mm.
Femur, length.....	160 mm.
Tibia, length.....	133 mm.
Tarsus, height at external angle to inferior face of euboid.....	34 mm.
Metatarsal II, length.....	36 mm.
Metatarsal III, length.....	53 mm.
Metatarsal IV, length.....	56 mm.
Metatarsal V, length.....	42 mm.
Phalanges, 2nd digit, length.....	45*mm.
Phalanges, 3rd digit, length.....	48 mm.

#### SUMMARY OF THE MORE IMPORTANT POINTS OF COMPARISON BETWEEN PHENACOCÆLUS, MERYCOIDODON, EPOREODON, AND LEPTAUCHENIA.

The foregoing comparative description of *Phenacocælus* with *Leptauchenia* and *Merycoïdodon* was undertaken with the purpose of ascertaining the relationship between these three genera, especially between *Phenacocælus* and *Leptauchenia*.

\*The phalanges were not found in position and their association with the pes should not be regarded as entirely positive.



For greater convenience a summary of the more important points of differences and the osteological similarities between *Phenacocælus* and other genera may be expressed as follows:

*Phenacocælus* resembles *Merycoidodon* more or less closely, throughout the entire skeletal structure. The two genera are alike, (1) in having the dentition numerically as well as in general form, quite similar; (2) in having a short facial region and an elongated cranium (cranium especially long in *Phenacocælus*); (3) by having deep lachrymal pits; (4) by having overhanging nasals; (5) by the location of the infraorbital foramen above P<sup>3</sup>; (6) by having the temporal ridges of similar shape and quite alike in the degree of development; (7) by a general similarity of the detailed structure of the vertebral column; (8) by a similarly large thoracic cavity; (9) by a similarity in most parts of the structure of the limbs; (10) by a general similarity of the manus (except the absence of the pollex in *Phenacocælus*).

*Phenacocælus* differs from *Merycoidodon culbertsoni*: (1) in having the skull proportionally broader and shorter; (2) in having the orbits directed more upward; (3) by the presence of fronto-nasal vacuities; (4) by the enlargement of the lachrymal pits and the indication of facial vacuities; (5) by having deep pits on posterior face of the occipital plate; (6) by the hypsodont cheek-dentition; (7) by having the tympanic bulla of very large size and extending much below the glenoid process; (8) by the feebly developed and low sagittal crest; (9) by the less transverse expanse of the transverse process of the atlas; (10) by the greater vertical and smaller transverse diameters of the neural spines of the anterior dorsals; (11) by having one more dorsal vertebra, and one less lumbar vertebra; (12) by having the carpus proportionally and actually higher; (13) by having the tibia shorter, heavier, and the shaft of somewhat different shape; (14) by having the pes relatively shorter and broader.

In consulting the literature I find the most complete description of *Eporeodon* from the upper Oligocene in the Proceedings of the American Philosophical Society Vol. XXI, 1884, pp. 514-517. In checking up the material of *Phenacocælus* in the Carnegie Museum with the above mentioned description by Professor E. D. Cope I find a number of anatomical similarities in *Eporeodon* and *Phenacocælus*, which are quite naturally to be expected in forms of the same family. The minor differences in the two genera in question are perhaps of an equal number to the similarities. Of the major differences the following may be mentioned: Cope describes a well defined pre-orbital fossa and frontal foramina as present in *Eporeodon tri-*

*gonocephalus*, but he speaks of no indication of facial or fronto-nasal vacuities, which are very characteristic of *Phenacocælus*.

In *Eporeodon socialis* Marsh, (See Fifth Annual Report U. S. Geol. Surv., 1885, p. 299, figs. 128-129) we learn that the length of the fore foot is approximately the same as in *Phenacocælus*, while the hind foot in *E. socialis* is 22 mm. longer. Mc. III in the latter species is 5 mm. longer, Mt. IV, 8 mm. longer, while the height of the carpus is actually less in *Eporeodon* than in *Phenacocælus*. When checked up with the foot-structure of *Merycoidodon culbertsoni* it is found that all the above measurements of *Eporeodon socialis* correspond much better with those in *Merycoidodon culbertsoni*. The remains of both *Eporeodon socialis* and *E. trigonocephalus* are of larger animals than *Phenacocælus*. From the information derived from the literature it may be inferred, that *Eporeodon*, as known, had not specialized in the direction of *Phenacocælus* to a sufficient degree anatomically, to lead us to consider that genus as directly in the phylogenetic line of *Phenacocælus*<sup>13</sup>.

*Phenacocælus* resembles *Leptauchenia*: (1) in the broadening and shortening of the skull; (2) in the tendency of the orbit, to be upward directed; (3) in the presence of fronto-nasal foramina or openings; (4) in having reduced premaxillaries; (5) in the shortening of the facial region; (6) in the enlargement of the lachrymal pits and the presence of facial vacuities; (7) in the hypsodont cheek-dentition and other similarities in the construction of these teeth; (8) in having the tympanic bulla of very large size and extending much below the postglenoid process; (9) in having the infraorbital foramen above P<sup>3</sup>; (10) in having the same number of dorsal and lumbar vertebræ; (11) in having a large thoracic cavity; (12) by having a similar broad and deep pelvic cavity; (13) by the general similarity of the greater parts of the structure of the limbs and feet.

*Phenacocælus* differs from *Leptauchenia* (1) in having larger and more numerous incisors, with the upper canine less rounded in cross-section; (2) in a more feebly developed sagittal crest, and a longer skull; (3) by having more overhanging nasals; (4) by having large and deep lateral excavations on the occipital plate; (5) by a narrower and more backward projecting occiput, together with less developed temporal crests; (6) by a relatively smaller external ear placed lower down; (7) by a smaller development of the dorsal arch of the atlas, and the absence

<sup>13</sup>The restoration of *Eporeodon socialis* recently published by Thorpe (Amer. Jour. Sci., Vol. II, 1921, p. 309) seems to show that *E. socialis* was similar to *Merycoidodon culbertsoni*. Loomis regards the skeletons of *Merycoidodon* and *Eporeodon* as closely similar (See Bull. Amer. Mus. Nat. Hist., Vol. LI, 1924, p. 9). Finally, if Thorpe's contention proves true that the sediments on the North Fork of the John Day are of later origin than the typical John Day, *Eporeodon trigonocephalus* is advanced to a horizon, which is nearer contemporaneity with *Phenacocælus*; (See Amer. Jour. Sci., 1921, (5) Vol. 2, p. 951).

of the canal for the vertebral artery, which perforates the base of the transverse process; (8) by relatively lighter cervical vertebræ, due to the relatively smaller head; (9) by the relatively greater antero-posterior and smaller transverse diameter of the neural spines of the anterior dorsal vertebræ; (10) by a much less developed tubercle for the attachment of the internal humeral part of the triceps on the olecranon process of the ulna; (11) by a relatively shorter and heavier tibia, different shape of its shaft; (12) by having a shorter and broader hind foot.

#### THE SYSTEMATIC POSITION OF PHENACOCÆLUS.

From the foregoing discussion it is safe to assume that *Phenacocælus* is a member of the extinct North American family *Agriochæridæ*. At the present time it is, however, difficult to point out the phylogenetic ancestry of *Phenacocælus* with any degree of certainty. In many respects the Oligocene genus *Merycoidodon* is sufficiently closely related to be regarded as in the line leading to *Phenacocælus*. For instance: the dentition, the short face, and elongated cranium, the large thoracic cavity and the general structure of the limbs and feet of *Merycoidodon* are characters very like those shown in *Phenacocælus*. However, a critical and detailed comparison of the bony structure of these two genera points rather to parallelism than to direct phylogenetic relationship. In no species of *Merycoidodon* known to the writer have we any indication of such important features, which are found in *Phenacocælus*, as the fronto-nasal vacuities, the enlargement of the preorbital foramen, and especially the tendency toward the formation of facial vacuities,<sup>14</sup> the height of the carpus, the different details of the construction of the tibia, and the short hind foot. In the limbs and feet of *Phenacocælus* are important characters, which we are not now able to compare with genera and species imperfectly known from the lower Oligocene. The shortening of the hind foot in *Phenacocælus* seems to be more in line with the condition found in *Agriochærus* than in any other early genus now known. The enormously inflated tympanic bulla is analogous to that in *Agriochærus*, *Merycoidodon bullatus*, and *Limnenetes platyceps* of the early Oligocene Oreodonts. We may then conclude that the direct ancestral line of *Phenacocælus* had in the early Oligocene time established characters along an entirely independent line, paralleling such genera as *Agriochærus*, *Merycoidodon*, and *Limnenetes*. Nor should we forget that comparatively little field-work has been done in the way of collecting the smaller fossil remains in the basal Oligocene. When we consult such discriminatory work as

<sup>14</sup>In a recent publication (Amer. Jour. Sci., (5) Vol. II, 1921, p. 109) Thorpe describes *Paroreodon marshi* as having facial vacuities in advance of the orbits.

that of Leidy,<sup>15</sup> Douglass,<sup>16</sup> Loomis,<sup>17</sup> and others it becomes quite patent that we may yet find Oreodonts somewhere in the basal horizons of the Oligocene which probably will furnish just such anatomical points as we may expect to discover in forms ancestral to *Phenacocælus* and *Leptauchenia*.

*Phenacocælus* and the phylum of *Leptauchenia-Cyclopidius* have no especially close relationship, but parallel one another more closely. This is indicated by the many cranial similarities; *i. e.*, the fronto-nasal vacuities, the position of the orbit, the size of the tympanic bulla, &c., together with other features, namely: the numerical identity of the vertebral formula, the large thoracic and pelvic cavities. The limbs and feet of *Leptauchenia* are on the whole more like those of *Merycoïdodon* than of *Phenacocælus*. One prominent feature of the fore limb in *Leptauchenia* is the great development of the antero-internal angle of the proximal end of the olecranon process of the ulna. This tubercle indicates a strong attachment for a branch of the extensor muscles of the fore arm, which is not nearly as well indicated in *Phenacocælus*, or any other known Oreodont.

The aquatic habit of *Leptauchenia* and *Cyclopidius* advocated by Professor Cope (Proc. Amer. Philos. Soc., XXI, 1884, p. 547) appear to be doubted by Dr. Sinclair, for the reason that the construction of the feet is apparently for cursorial habit on firm ground, and Sinclair disagrees with Cope in regarding the skull as pointing toward aquatic life on part of the animal. Sinclair believes that the geological formation in which *Leptauchenia* is found (heavy bedded clays) is a safer clue to the habit of the creature than the structure of its skeleton<sup>18</sup> (*op. cit.*, XLIX, 1910, p. 198).

Many features displayed in the osteology of *Phenacocælus*, especially those of the cranium, point to relationship with *Leptauchenia* and *Cyclopidius*, but the specialization of the latter genera shows, on the whole, a greater separation from the earlier types of the family than is the case in *Phenacocælus*.

The *Leptauchenia*-like features of the cranium in *Phenacocælus* possibly

<sup>15</sup>"The Extinct Mammalian Fauna of Dakota and Nebraska." Jour. Acad. Nat. Sci., Vol. VII, 1869, pp. 104-106. Leidy describes three species: "*Oreodon*" *affinis*, "*O*" *hybridus*, and "*O*" *bullatus* supposed to be from the lower Oligocene of Nebraska and Dakota.

<sup>16</sup>Trans. Amer. Philos. Soc., Vol. XX, 1901, pp. 260, 262. Douglass describes *Limnenetes platyceps* and *L. anceps* from the basal Oligocene of Montana.

<sup>17</sup>Ann. Car. Mus. Vol. XV, 1924, p. 370-373. Loomis erects *Oronetes* as a genus using the type of *Limnenetes anceps* Douglass and associated material in the Carnegie Museum as the basis of his description.

<sup>18</sup>Thorpe in a recent publication (Jour. Mammalogy, VI, No. 2, May, 1925, p. 73) follows Cope in advancing the idea that *Leptauchenia* was aquatic from the peculiar position of the eye, ear, and other features of the skull.

suggest the same mode of life as that of *Leptauchenia*, whatever it was, while the limbs, especially the hind limb, are of a decidedly heavier type and the hind foot is relatively shorter, which plainly indicates an animal having less speed than the *Leptauchenia* and perhaps more closely confined to denser vegetation, as a means of protection.

#### POSTSCRIPT.

Since the manuscript of the foregoing paper was prepared in 1909 and revised in 1914, much work has been done on the Oreodonts. Loomis of Amherst and Thorpe of the Peabody Museum, have contributed a great many papers from time to time. A study by Loomis of the cranial, and especially the dental structure of the premolars of the Artiodactyla in general, and the Oreodontidæ in particular, resulted in the division of that family into five distinct phylogenetic groups. While it is true that the axial skeleton (excepting the skull) and the appendicular skeleton of the Oreodonts from the earliest to the latest forms, are all quite generalized in character, we learn from careful detailed study of complete skeletal material that there are definite characters, which together with those of the cranium, may prove of greater value in phyletic study than is now generally admitted. From the comparative study of the three genera, *Merycoidodon*, *Phenacocælus*, and *Leptauchenia*, with which the foregoing pages chiefly deal, there is for instance revealed the fact that *Phenacocælus* had the hind limbs, especially the hind feet, more nearly like those of *Agriochærus* than any other Oreodont, of which those parts are known, and would no doubt be placed in phylogenetic relationship with that genus, if no other parts of its structure were known. Loomis (*l. c.* p. 15) places *Phenacocælus* in the line of more direct descent from *Eporeodon*, and also advances the idea that *Phenacocælus* belongs to the line of *Ticholeptus* because of the relatively slight change in the structure of the teeth.<sup>19</sup> While my limited comparative study of the Oreodonts does not at this time warrant proposing any change in Dr. Loomis' proposed scheme, I, however, am undisturbed in my views as to the systematic position of *Phenacocælus*, which I reached, many years ago. When the full description of the skeleton of *Eporeodon socialis*, promised by Thorpe<sup>20</sup> appears; when we know more fully the skeletal structure of other species of *Eporeodon*, as well as of other genera from the John Day and the upper Oligocene; when we get more complete information than is furnished by Thorpe<sup>21</sup>, on the extensive material

<sup>19</sup>Bull. Amer. Mus. Nat. Hist., Vol. LI, p. 12, 1924.

<sup>20</sup>Amer. Journal Science, (5) Vol. VII, 1924, p. 224.

<sup>21</sup>Ibid. Vol. II, December 1921, p. 339.

of *Merycoidodon affinis* in the Yale Museum; when we have more complete knowledge of the genera of this family already found in the basal Oligocene, and others, perhaps yet to be discovered somewhere in the lower horizons of the Oligocene, we shall be in possession of much needed and welcome information in support, or non-support, of our hypothesis and guesses in connection with the phylogeny of the Oreodontidæ.



## EXPLANATION OF PLATE XVI.

All figures from 1 to 39 inclusive are from the type specimen of *Phenacocælus typus* No. 1263, except figure 31 which is a view of the paratype of *Phenacocælus typus* No. 1335.

Figs. 1-7. Views of cervical vertebræ, left side.

Fig. 8. Dorsal view of atlas.

Fig. 9. Ventral view of atlas.

Figs. 10-29. Views of vertebral column from the first dorsal to and including a portion of the first sacral in their relative order of sequence; seen from the left side.

Fig. 30. Views of anterior caudal vertebræ; left side.

Fig. 31. Skull and lower jaws of *Phenacocælus typus*; paratype No. 1335. View of right side.

Fig. 32. Scapula; external face.

Fig. 33. Humerus; anterior face.

Fig. 34. Radius and ulna; anterior face.

Fig. 35. Fifth and sixth lumbar vertebræ and a portion of the first sacral vertebra as found in position; view from above.

Fig. 36. Right side of pelvis.

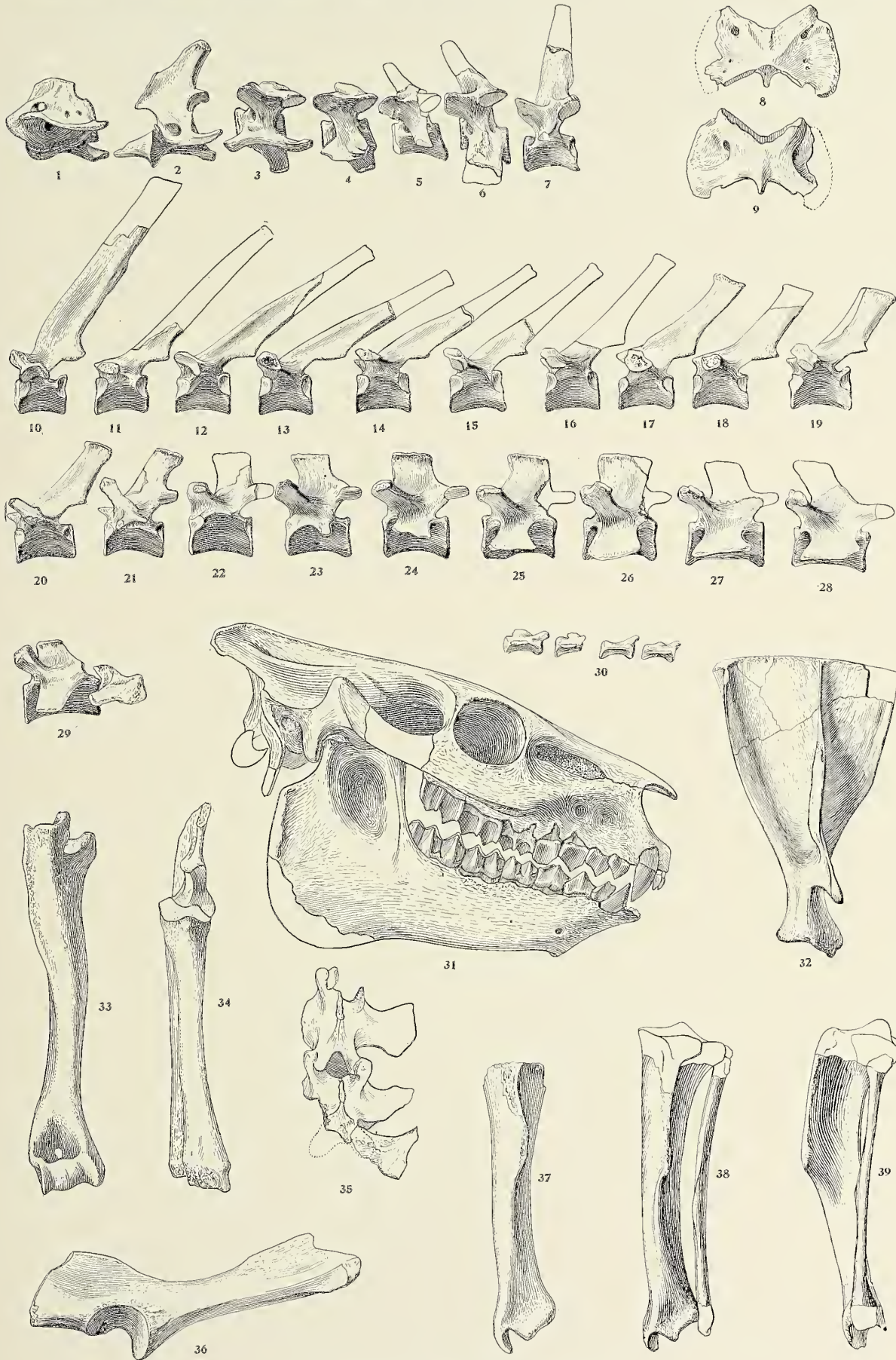
Fig. 37. Left tibia; anterior face.

Fig. 38. Left tibia and fibula; anterior face.

Fig. 39. Left tibia and fibula; fibular face.

All figures one-half natural size.





For explanation see opposite page.

## EXPLANATION OF PLATE XVII.

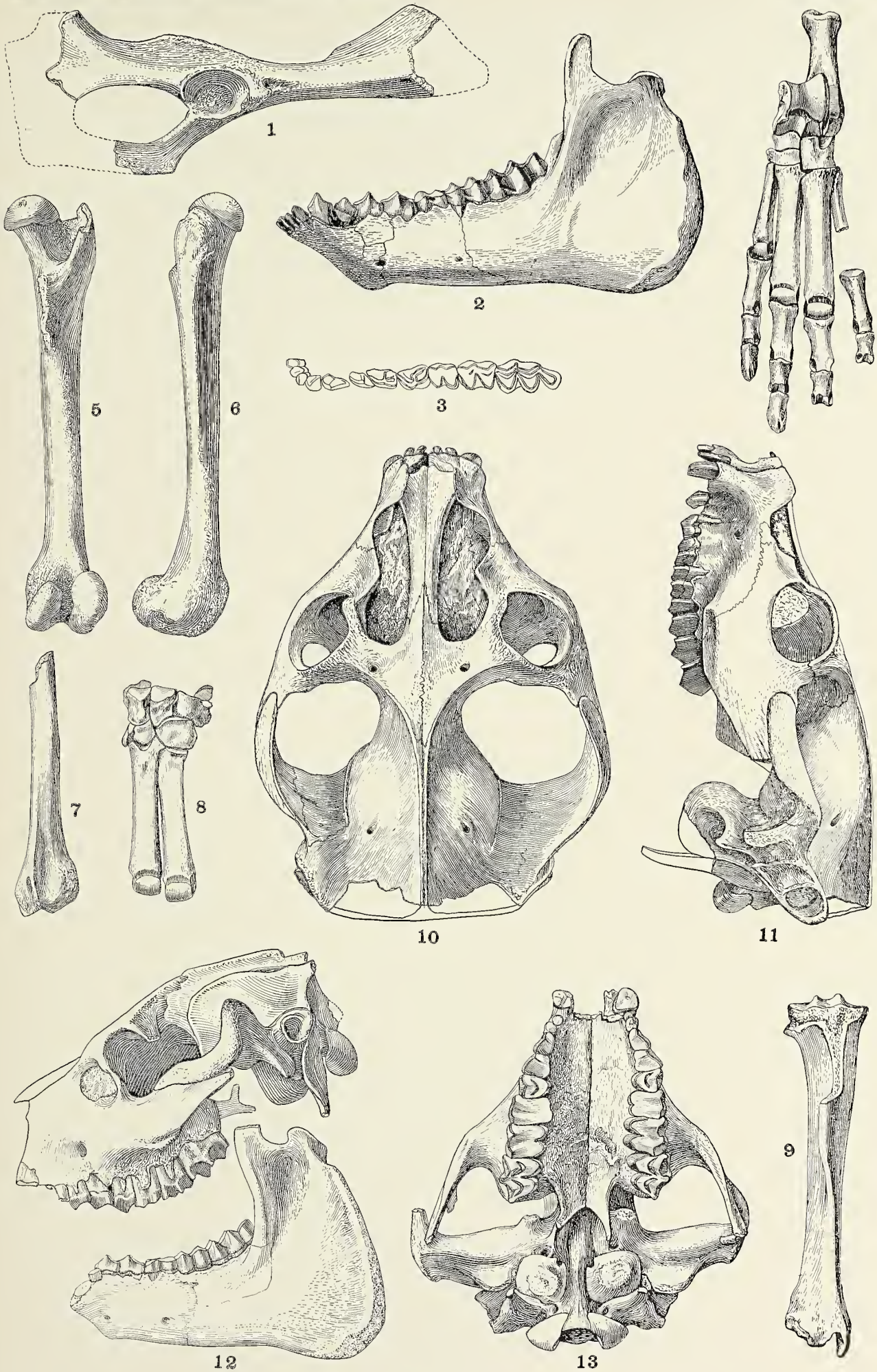
- Fig. 1. Upper cheek-teeth, *Phenacocælus typus*, paratype No. 1335.  
Fig. 2. Lower cheek-teeth, *Phenacocælus typus*, paratype No. 1335.  
Fig. 3. Palmar face of right manus, *Merycoidodon culbertsoni*, No. 1391.  
Fig. 4. Dorsal face of right manus, *Merycoidodon culbertsoni*.  
Fig. 5. Dorsal face of right manus, *Phenacocælus typus*, No. 1263.  
Fig. 6. Palmar face of right manus, *Phenacocælus typus*, No. 1263.  
Fig. 7. Left calcaneum and astragalus, dorsal face, *Phenacocælus typus*, No. 1263.  
Fig. 8. Left calcaneum and astragalus, plantar face, *Phenacocælus typus*, No. 1263.  
Fig. 9. Plantar face of pes, *Phenacocælus typus*, No. 1263.  
Fig. 10. Dorsal face of pes, *Phenacocælus typus*, No. 1263.  
Fig. 11. Top of skull, *Phenacocælus typus*, paratype No. 1276.  
Fig. 12. Palatal view of skull, *Phenacocælus typus*, paratype No. 1276.

All figures two-thirds of nature.

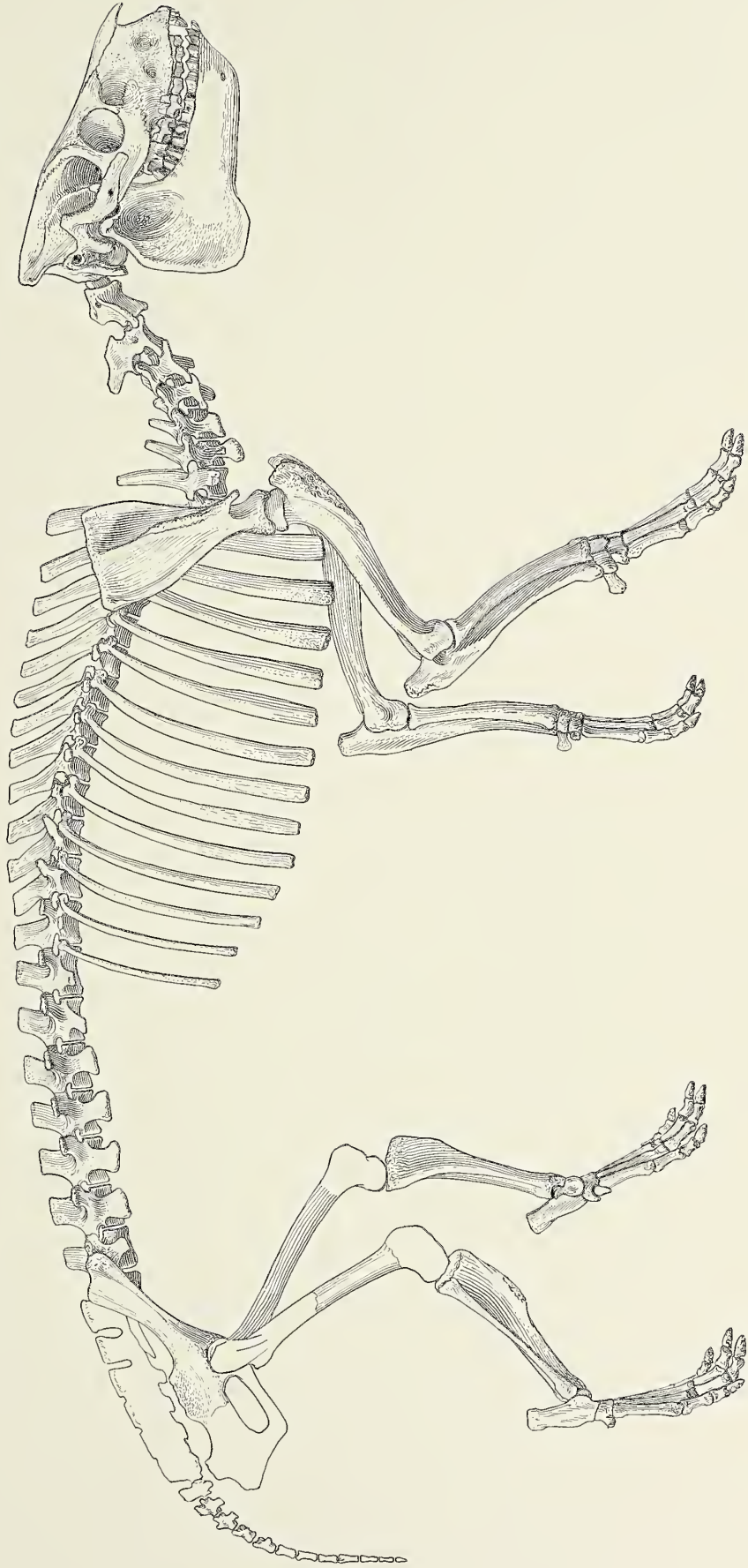
## EXPLANATION OF PLATE XVIII.

- Fig. 1. Portion of right side of pelvis, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 2. Left lower jaw, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 3. Lower dentition in outline, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 4. Dorsal face of pes, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 5. Posterior face of femur, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 6. Fibular face of femur, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 7. Anterior face of radius, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 8. Dorsal face of manus, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 9. Anterior face of right tibia, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 10. Top view of skull, *Cyclopidius* No. 1307.  
Fig. 11. Side view of skull, *Cyclopidius*, No. 1307.  
Fig. 12. Skull and jaws, view of left side, *Phenacocalus typus*, paratype, No. 1278.  
Fig. 13. Palatal view of skull, *Phenacocalus typus*, paratype, No. 1278.

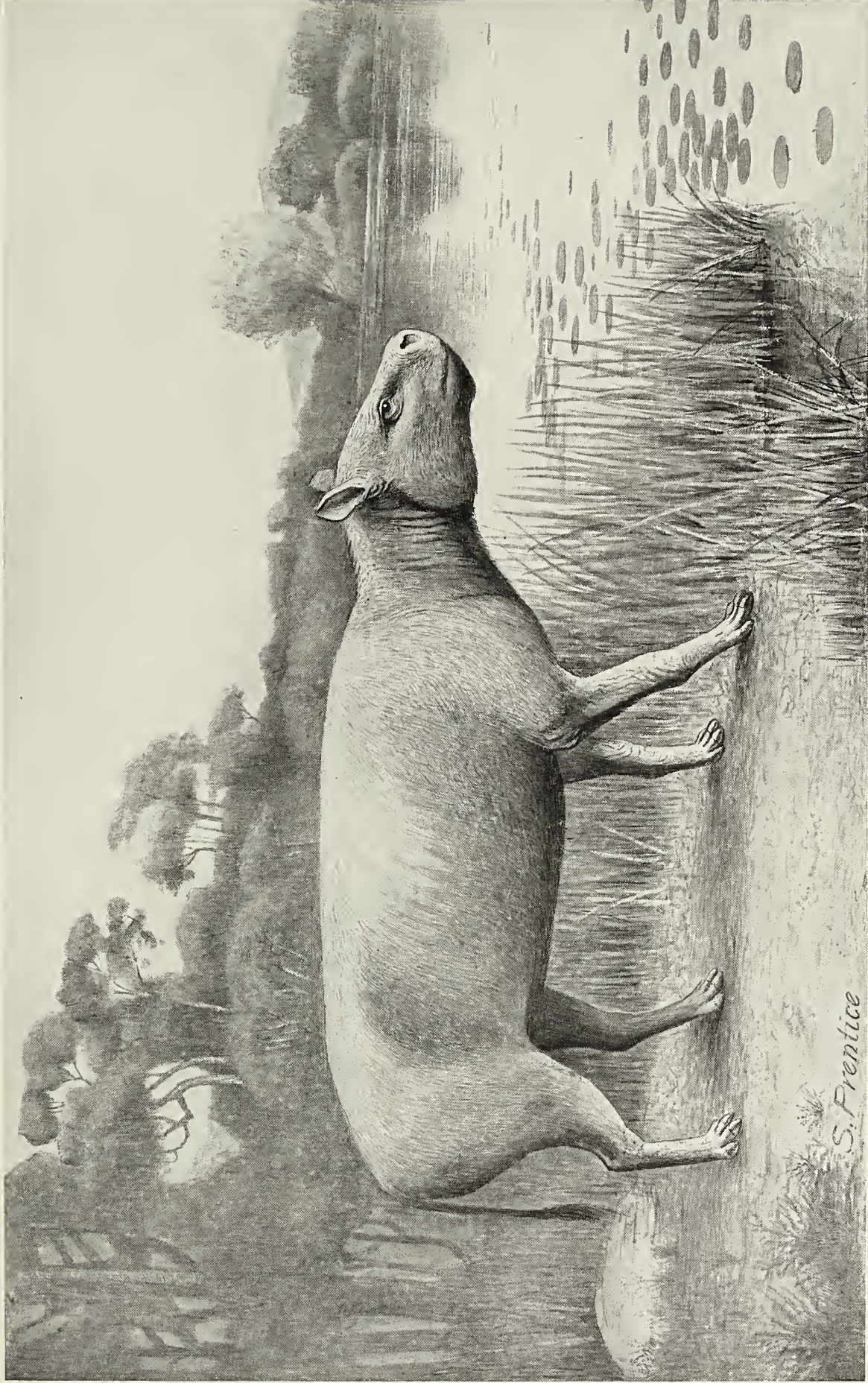
All figures one-half of nature, except figure 10 and 11 which are natural size.



For explanation see opposite page.



Articulated Skeleton of *Phenacocetus typus* Peterson.  
Type of the genus and species (C. M. Cat. Vert. Foss., No. 1263). One-fourth natural size.



*Phocaocelus typus* Peterson.  
Restoration of the Type of the Genus (C. M. Cat. Vert. Foss., No. 1263). One-sixth natural size.